
Nearshore Biological Community Patterns Related to Lake Michigan Shorelines



Prepared by:
Reuben R. Goforth, Ph.D. and Stephanie M. Carman

Michigan Natural Features Inventory
P.O. Box 30444
Lansing, MI 48909-7944

For:
Michigan Department of Environmental Quality
Office of the Great Lakes and Coastal Zone Management Unit
and
National Oceanographic and Atmospheric Administration

January 2005

Report Number 2005-01
DEQ-CZM Project #03-6217-08



Nearshore Biological Community Patterns Related to Lake Michigan Shorelines

Prepared by:
Reuben R. Goforth, Ph.D.^a and Stephanie M. Carman^b

^aMichigan Natural Features Inventory
P.O. Box 30444
Lansing, MI

^bConservation Services Division
New Mexico Department of Game and Fish
PO Box 25112
Santa Fe, NM 87504

For:
Michigan Department of Environmental Quality
Office of the Great Lakes and Coastal Zone Management Unit
and
National Oceanographic and Atmospheric Administration

January 2005

Report Number 2005-01

DEQ-CZM Project #30-6217-08



Table of Contents

INTRODUCTION	1
METHODS	3
<i>Study Sites</i>	<i>3</i>
<i>Physicochemical Habitat and Biological Surveys</i>	<i>3</i>
<i>Spatial Data</i>	<i>4</i>
<i>Statistical Analysis</i>	<i>5</i>
RESULTS	5
<i>Summary</i>	<i>5</i>
<i>Local Shoreline Type Analyses</i>	<i>5</i>
<i>Spatial Analyses</i>	<i>13</i>
DISCUSSION	24
SUMMARY	27
ACKNOWLEDGEMENTS	27
LITERATURE CITED	27
COLOR PLATES	31

List of Tables

Table 1. Sample dates for nearshore areas surveyed in Lake Michigan during the summers of 2003 and 2004.....	6
Table 2. Mean (± 1 S.E.) physicochemical measures for nearshore areas adjacent to modified and intact shorelines of Lake Michigan. Water temperature, dissolved oxygen, conductivity, and pH measures are based on measurements taken at 2.0 m water depth along the 3.0 m depth contour of study sites.....	6
Table 3. Mean (± 1 S.E.) benthic macroinvertebrate densities (number of individuals/m ²) for nearshore areas adjacent to modified and intact shorelines of Lake Michigan. Samples were collected during summers 2003 and 2004 using a Petite Ponar® grab (0.023m ²). Study sites include St. Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and south of the Ludington pump storage station (LU). Taxonomic groups include the dipteran Chironomidae (sub-families Chironominae (Chiro); Orthocladiinae (Ortho); Podonominae (Podo); Prodiamesinae (Prodi); and Tanypodinae (Tanypod); and the tribe Tanytarsini (Tanytar)), the dipteran Ceratopogonidae (Cerato), oligochaete worms (Oligo), water mites (Mites), dreissenid mussels (Dreis), and total benthic macroinvertebrate (Tot_Ben).....	7
Table 4. Mean densities (± 1 S.E.) of native and non-native zooplankton taxa observed in vertical plankton tows collected along the 3 m depth contour of nearshore waters along Lake Michigan shorelines, including Saint Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and Ludington (LU)..	8
Table 5. Mean (± 1 SE) catch per unit effort (CPU) measures for fish species observed in beach seines during surveys of shallow water fish communities associated with Great Lakes shoreline areas. Study sites include St. Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and south of the Ludington pump storage station (LU).....	9
Table 6. Mean (± 1 SE) catch per unit effort (CPU) measures for fish species observed in gill nets during surveys of nearshore fish communities associated with eight Great Lakes shoreline areas. Study sites include St. Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and south of the Ludington pump storage station (LU).....	9
Table 7. Percentage of 1.0 km shoreline buffers comprised of urban land uses along the eastern Lake Michigan shoreline. Buffers include a 5 km-long shoreline reach encompassing each study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shoreline reaches updrift from each study site.....	16
Table 8. Number of shore structures within 1.0 km shoreline buffers along the eastern Lake Michigan shoreline. Buffers include a 5 km-long shoreline reach encompassing each study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shoreline reaches updrift from each study site.....	16
Table 9. Results of linear regressions between biological community measures and the spatial extent of urban land use (i.e., % buffer area as urban) within 1-km shoreline buffers defined at multiple spatial scales. Buffers included a 5 km shoreline encompassing the study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shorelines updrift from the study sites. Biological community measures are defined in the Methods section of the text. Statistically significant relationships between biological community parameters and the number of shore structures within a given buffer context are highlighted in gray.....	17
Table 10. Results of linear regressions between biological community measures and the number of shoreline structures within 1-km shoreline buffers defined at multiple spatial scales. Buffers included a 5 km shoreline encompassing the study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shorelines updrift from the study sites. Biological community measures are defined in the Methods section of the text. Statistically significant relationships between biological community parameters and the number of shore structures within a given buffer context are highlighted in gray.....	18

List of Figures

Figure 1. Study site locations along the eastern shore of Lake Michigan.	3
Figure 2. Mean (± 1 S.E.) total densities of A) benthic macroinvertebrates (number of individuals/m ² , and B) zooplankton (number of individuals/m ³ , segregated by shoreline type (modified and intact) for samples collected along the 3 m depth contour of eastern Lake Michigan during summer 2003 and 2004.....	10
Figure 3. Mean (± 1 S.E.) densities of benthic macroinvertebrate taxonomic groups segregated by shoreline type (modified and intact) for samples collected along the 3 m depth contour of eastern Lake Michigan during summer 2003 and 2004. Taxonomic groups include the chironomid subfamilies Chironominae (A), the Orthocladinae (B), and Tanypodinae (C) and oligochaete worms (D).....	11
Figure 4. Mean (± 1 S.E.) densities of zooplankton taxonomic groups segregated by shoreline type (modified and intact) for samples collected along the 3 m depth contour of eastern Lake Michigan during summer 2003 and 2004. Taxonomic groups include Cyclopoida (A), Calanoida (B), Cladocera (C) and Rotifera (D).	12
Figure 5. Mean (± 1 S.E.) catch per unit effort (CPU) for shallow water fish captured in beach seine hauls at sites segregated by shoreline type (modified and intact) in eastern Lake Michigan during summer 2003. Individual species at >3 study sites include <i>Alosa pseudoharengus</i> (alewife, Alew), <i>Fundulus diaphanus</i> (banded killifish, Baki), <i>Rhinichthys cataractae</i> (longnose dace, Lodo), and <i>Neogobius melanostomus</i> (round goby, Rogo). Groupings include overall shallow water piscivores (SWPis), planktivores (SWPlk), benthivores (SWBen), insectivores (SWIns), native fish (SWNat) and introduced fish (SWInt).....	14
Figure 6. Mean (± 1 S.E.) catch per unit effort (CPU) for nearshore fish captured in gill net hauls at sites segregated by shoreline type (modified and intact) in eastern Lake Michigan during summer 2003. Individual species and families at >3 study sites include <i>Aplodinotus grunniens</i> (freshwater drum, Frdr), <i>Dorosoma cepedianum</i> (gizzard shad, Gish), catostomids (Cato), salmonids (Salm), and percids (Perco). Groupings include overall nearshore piscivores (SWPis), planktivores (SWPlk), benthivores (SWBen), native fish (SWNat) and introduced fish (SWInt).	15
Figure 7. Relationships between A) total shallow water fish catch per unit effort (SWTot) and urban land use within the 10 km updrift landscape context, B) shallow water planktivorous fish CPU (SWPlk) and urban land use within the 50 km updrift landscape context, C) shallow water native fish CPU (SWNat) and urban land use within the 10 km updrift landscape context, and D) shallow water introduced species CPU (SWInt) and urban land use within the 10 km updrift landscape context.	19
Figure 8. Relationships between A) total shallow water fish catch per unit effort (SWTot) and the number of shore structures within the 100 km updrift landscape context, and B) total nearshore fish catch per unit effort and the number of shore structures within the 50 km updrift landscape context.	20
Figure 9. Relationships between A) shallow water insectivorous fish catch per unit effort (SWIns) and the number of shore structures within the 100 km updrift landscape context, B) shallow water benthivorous fish CPU (SWBen) and the number of shore structures within the 100 km updrift landscape context, C) shallow water native fish CPU (SWNat) and the number of shore structures within the 100 km updrift landscape context, and D) shallow water introduced species CPU (SWInt) and the number of shoreline structures within the 10 km updrift landscape context.	21
Figure 10. Relationships between A) nearshore piscivorous fish catch per unit effort (NSPis) and urban land use within the 10 km updrift landscape context, and B) nearshore planktivorous fish catch per unit effort and urban land use within the 100 km updrift landscape context.	22

List of Figures (cont.)

Figure 11. Relationships between A) nearshore piscivorous fish catch per unit effort (NSPis) and the number of shore structures within the 100 km updrift landscape context, B) nearshore benthivorous fish CPU (NSBen) and the number of shore structures within the local landscape context, C) nearshore native fish CPU (NSNat) and the number of shore structures within the 100 km updrift landscape context, and D) nearshore introduced species CPU (NSInt) and the number of shoreline structures within the 50 km updrift landscape context.....23

List of Color Plates

Plate 1. An example of a modified shoreline near Saint Joseph, Michigan, with commercial land use and extensive shore structure development. Loss of vegetation on areas of the bluff have caused high levels of erosion and soil loss.	32
Plate 2. An example of a largely intact shoreline near Ludington, Michigan.	32
Plate 3. Removal of benthic samples from the Petite Ponar dredge prior to preservation in ethanol.	33
Plate 4. Deployment of the zooplankton net to collect vertical plankton tows at the 3.0 m depth contour of study sites.	33
Plate 5. Zebra mussel clusters and individuals attached to a gastropod shell and leaves of <i>Vallisneria americana</i> found in the drowned river mouth of the Pere Marquette River where it joins with Lake Michigan.	34

INTRODUCTION

Nearshore zones play key roles in Great Lakes ecology. They link terrestrial and aquatic environments, facilitating the exchange of energy and materials between coastal and pelagic ecosystems. They also provide spawning, rearing, foraging, and migratory habitats essential for most Great Lakes fishes, including many recreationally and commercially important species (Goodyear et al. 1984; Lane et al. 1996a; Lane et al. 1996b). Other taxa, such as benthic invertebrates, zooplankton, and non-game fish species, are also characteristic of nearshore zones (e.g., Jude and Tesar 1985; Evans 1986; Thayer et al. 1997; Madenjian et al. 2002; Dettmers et al. 2003) where they support Great Lakes fisheries and contribute to processes that support other ecosystem services, such as potable water supplies (Daily et al. 1997). Nearshore zones are therefore of much greater significance than their comparatively limited spatial extent would suggest (Goforth and Carman *in press*). However, they have been the subject of comparatively few studies (e.g., Jude and Tesar 1985; Brazner and Beals 1997; Brazner 1997; Garza and Whitman 2004; Goforth and Carman *in press*), and their ecology and dynamics remain poorly understood, especially in exposed shore areas (Randall and Minns 2002). This limited understanding of nearshore ecology looms large as a serious impediment to ecosystem management and restoration of Great Lakes ecosystems (Goforth and Carman 2003).

It is clear that Great Lakes researchers, managers, planners, and conservationists have much work to do where nearshore science is concerned. Very few historical benchmarks exist, and locations within major regions of the Basin that can be considered as reference conditions are generally lacking (e.g., southern Lake Erie, southern Lake Michigan, etc.). Therefore, understanding nearshore dynamics based on contemporary studies presents many challenges. Although the Great Lakes are large bodies of water with complex currents that would seemingly dilute inputs from terrestrial sources, the proximity of nearshore zones to shorelines and their role as an ecotone bridging terrestrial and pelagic environments makes them susceptible to the influences of human land uses in coastal areas. Indeed, multiple stressors related to urban, industrial, and residential development of shorelines have dramatically altered many Great Lakes nearshore environments (Steedman and Regier 1987; Busch and Lary 1996; Kelso and Cullis 1996; Kelso et al. 1996). The resulting changes in physicochemical properties have been implicated as driving factors in the widespread alteration of biological communities and ecological functions in the Great Lakes (Whillans 1979; Krieger 1984; Kelso et al. 1996; Brazner and Beals 1997). For example, physicochemical habitat

change has been identified as an important factor in structuring fish communities in coastal wetland habitats (Leslie and Timmins 1994; Brazner and Beals 1997), and it is likely to be a significant contributing factor in structuring macroinvertebrate and zooplankton communities in nearshore areas as well (Goforth and Carman *in press*). There is therefore little doubt that the wholesale physical and chemical alteration of nearshore zones represents a significant impediment to the study and management of nearshore resources.

Non-native taxa have substantially influenced native aquatic communities in the Great Lakes via food web disruptions, competition for resources (e.g., prey and physical habitat), and predation (Mills et al. 1993; Busch and Lary 1996; Ricciardi and McIsaac 2000; Vanderploeg et al. 2002; Ratti and Barton 2003). For example, *Dreissena polymorpha* and *D. bugensis* have influenced benthic invertebrate communities (positively and negatively) by increasing colonizable surface area (e.g., Botts et al. 1996; Karatayev et al. 1997; Ricciardi et al. 1997; Stewart et al. 1998) and redirecting sources of primary productivity to benthic habitats via deposition of pseudofeces (Izvekova and Lvova-Katchanova 1992; Roditi et al. 1997; Thayer et al. 1997; Stewart et al. 1998). They have also indirectly competed with zooplankton (Dettmers et al. 2003) and the amphipod *Diporeia hoyi* (Dermott and Kerec 1997) for phytoplankton, thus redirecting energy from pelagic environments to benthic environments and disrupting food web structure (Vanderploeg et al. 2002). This change in food web dynamics is then projected to fish and other predators that have historically relied on greater access to benthic invertebrates now concealed in interstices of zebra mussel shells and zooplankton/prey fish that have realized a decreased source of primary productivity (i.e., phytoplankton) (McIsaac 1996; Haynes et al. 1999). Invasive species such as *Dreissena* sp. and *Neogobius* sp. have become well established in many nearshore areas of the Great Lakes, and thus present a second major impediment to understanding and managing Great Lakes nearshore ecosystems.

Goforth and Carman (*in press*) suggested that altered shorelines may encourage non-native species invasion success in adjacent nearshore areas. Such species are often habitat generalists that are able to adapt quickly to changing habitat conditions, especially when competing with specialist native taxa. While these findings were based on a pilot study, they nonetheless suggested the potential cumulative effects of physical, chemical, and biological stressors on native nearshore biological communities in nearshore environments. They also imply that management activities aimed at restoring Great Lakes nearshore habitats may have dual benefits in providing habitats preferred by native taxa that are

simultaneously less favorable to non-native taxa, providing native taxa with a competitive advantage and potentially addressing some of the industrial and economic issues related to non-native invaders. While native biological communities have been shown to become altered along shorelines with high levels of anthropogenic activity compared to intact shorelines (e.g., Brazner 1997; Brazner and Beals 1997; Goforth and Carman *in press*), complementary work to determine relationships between non-native communities and shoreline land use has not been performed to date.

Whether native or non-native, the structure of biological communities is governed by processes that result from interactions of biotic and abiotic factors operating over multiple spatial scales (Eadie and Keast 1984; Ricklefs 1987; Dunson and Travis 1991; Minns 1989). Aquatic ecologists have long recognized that local biological communities are linked to larger scale environmental factors via the influences of these factors on local habitats in streams (e.g., Hynes 1975; Vannote et al. 1980; Frissel et al. 1986). Many studies have demonstrated relationships between stream (e.g., Osborne and Wiley 1988; McMahon and Harned 1998) and lake (Whittier et al. 1988; Soranno et al. 1996) habitat characteristics and the extent of human land uses in surrounding watersheds. Similarly, land use composition of watersheds has also been implicated as influencing local biological communities in these systems, presumably in response to habitat changes resulting from landscape alterations (e.g., Reeves et al. 1993; Weaver and Garman 1994; Wichert 1995; Richards et al. 1996; Allan and Johnson 1997; Roth et al. 1997; Goforth et al. 2002). These studies demonstrate the great need for considering scale as a factor in managing aquatic ecosystems to promote long term resource viability and sustainability. As complex littoral environments, nearshore ecosystems are likely driven by similar multi-scale environmental factors of surrounding or adjacent landscapes, similar to relationships observed in stream (e.g., Allan and Johnson 1997; Richards et al. 1997) and inland lake (e.g., Soranno et al. 1996) ecosystems. Therefore, a multi-scale approach to assessment and management is warranted for these systems.

Relating Great Lakes nearshore communities to both local and larger scale landscape properties of adjacent shorelines has been the subject of few studies (e.g., Kelso and Minns 1996; Brazner and Beals 1997; Wei et al. 2004; Goforth and Carman *in press*). Meadows et al. (*in press*) suggested that local changes in shoreline land use and structure have cumulative impacts on local nearshore ecology via alterations in coastal substrate dynamics that influence habitat distribution and quality in nearshore zones. However, representation of fish species, especially large piscivores, at particular nearshore sites has also

been shown to be primarily related to regional factors (Kelso and Minns 1996; Brazner and Beals 1997). Such wide ranging and diadromous species are less likely to exhibit predictable community changes among specific locations because they are more successful in taking advantage of disparate habitats (Kelso and Minns 1996; McDowall 1996). On the other hand, some smaller, more short-lived fish species (e.g., cyprinids) appear to be more responsive to local habitat factors (Schindler 1987). Macroinvertebrates have been shown to be responsive to both local and landscape scale environmental properties in streams, so the scale at which they respond to environmental change is difficult to predict. Zooplankton distributions are often dependent upon prevailing currents, and may thus be more responsive to larger scale phenomena in Great Lakes nearshore zones. Regardless, it appears that nearshore ecosystems should be studied within a hierarchical spatial context in order to effectively identify the causal factors responsible for structuring resident biological communities (Duarte and Kalff 1990; Brazner and Beals 1997).

Associating aquatic communities with stressors related to urban and industrial activities within catchments can be difficult (Kelso et al. 1996). At the Great Lakes Basin scale, cumulative impacts of these stressors may be significant, although explicitly identifying these factors as causal is likely unachievable. A more tenable and manageable land area to explore as a causative agent influencing nearshore ecology is the shoreline. Shorelines may act very similarly to riparian zones of streams and rivers, acting as buffers to anthropogenic activity when they are intact and providing little to no protection from human land uses when they are fragmented or characterized by active land uses themselves (e.g., Weller et al. 1998; Gergel et al. 2002). In combination with prevailing currents that can carry materials from updrift areas, shorelines may operate over multiple spatial scales to influence biological communities at local sites. If such patterns do exist, they can provide potential landscape indicators for assessing ecological integrity of nearshore zones over much broader areas of the Basin and act as a foundation for alternative management of shorelines to enhance the long-term viability of nearshore ecosystems.

We sought to determine whether local nearshore biological community measures for native and non-native taxa were associated with local and larger scale shoreline environmental properties, including land cover composition and the number of shore structures present within specified geographic areas (e.g., revetments, groin fields, jetties, piers, etc). Our primary goal was to provide a comprehensive assessment of native and aquatic nuisance species (ANS) community responses to multi-scale shoreline environmental properties based on field

surveys of nearshore waters adjacent to local shorelines with high and low disturbance regimes. The primary hypothesis of this study was that fish, benthic invertebrates, and zooplankton native species/community densities and ANS are related to shoreline structure density and urban land use quantified over local and increasingly larger shoreline spatial contexts. We expected ANS densities would be higher and thus reflect greater invasion success in nearshore areas associated with locally degraded shorelines, while native taxa densities would be lower in these same areas. We also expected native community density measures to be negatively associated with shore structure densities measured over increasing spatial scales along shorelines, while ANS densities would be positively related to increases in shore structure numbers. Finally, we expected native fish, benthic, and zooplankton densities to be negatively related to the spatial extent of urban land uses quantified within 1-km wide shoreline reaches at progressively larger scales, while ANS densities would be positively related to higher urban land use contributions to these 1-km wide shoreline reaches.

METHODS

Study Sites

Study sites were located on the eastern shore of Lake Michigan between St. Joseph and Ludington, MI. We used a two-tiered selection process. Twelve potential sites were first chosen based on topographic map and aerial photograph (1:16,000 scale) interpretations. Topographic maps were used to identify shorelines with steep profiles suggesting moderate to high bluff shoreline types. Once the bluff areas were identified, we used aerial photographs to interpret land use and land cover along the shorelines. We identified six nearshore areas adjacent to modified (i.e., high levels of human activity and land use, Plate 1) bluff shorelines and six nearshore areas adjacent to largely intact (i.e., low levels of human land use and dominated by vegetated land covers and/or dunes, Plate 2) bluff shorelines. The second phase of the selection process involved site visits to assess local environmental characteristics and comparability of sites within treatment classes. Based on the site visits, we selected four of the six sites for each shoreline treatment class as study sites (eight sites total). The modified sites included nearshore areas south of Saint Joseph (SJ), north of Whitehall (WH), north of Muskegon at Pioneer Park (PP), and in the vicinity of Silver Lake State Park (SL) (Fig. 1). The intact sites included nearshore areas north of Saint Joseph at Mizpah Park (MP), south of Holland (SH), south of Pentwater adjacent to the Pere Marquette State Forest (PM), and south of Ludington (LU) (Fig. 1).

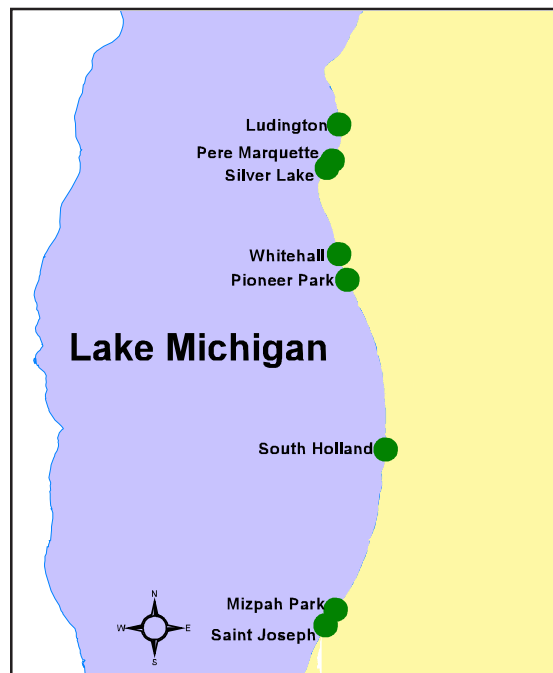


Figure 1. Study site locations along the eastern shore of Lake Michigan.

Study sites were visited once a year for two years (2003 and 2004) to sample local biological communities. At each site, three transects were established perpendicular to the shoreline during 2003 using a Garmin 12XL Global Positioning System (GPS) receiver (± 10 m accuracy). Transects were established at approximately 1.0 km increments along the shoreline at each site. Sampling stations coinciding with the 3.0 m water depth contour were established along each transect using the GPS. These transects and sampling stations provided a spatial framework for sampling that could be used during both project years.

Physicochemical Habitat and Biological Surveys

Physicochemical properties were only measured during summer 2003 due to difficulties with the digital meters that precluded consistent sampling of water chemistry during summer 2004. Temperature and dissolved oxygen were measured using a calibrated YSI-55 digital meter, and conductivity and pH were measured using an Oakton model pH/Con 10 digital meter. Turbidity was measured using a 200 mm Secchi disk (Fieldmaster®), and was defined as the depth at which the black and white quadrant color patterns on the disk could no longer be discerned visually at the surface. Temperature, dissolved oxygen, pH, and conductivity were measured at 2.0 m depth at each of the zooplankton/benthos sampling stations. Secchi depth was also determined at the sampling stations at sites where Secchi depth was < 3.0 m. For sites with less turbid waters, Secchi depth was determined at an offshore point along

the transect that was sufficiently deep enough to deploy the disk until it disappeared.

Benthic macroinvertebrate and zooplankton samples were collected at all sites during both years of the study. Three benthic invertebrate samples were collected at each sampling station using a Petite Ponar® grab (0.023 m², nine total samples/site). Benthic samples were sieved (0.5 mm, Newark Wire Cloth Co., Newark, New Jersey) to remove excess sand and silt, and the remaining sample contents were washed into a sample storage bottle using 95% ethanol (EtOH) (Plate 3). Organisms in benthic samples were later identified to the lowest practicable and meaningful taxonomic level in the laboratory. Benthic communities were described using measures of benthic macroinvertebrate total density (BMTD, number of individuals/m²), chironomid total density (CTD, number of individuals/m²), and densities of Chironominae, Orthocladiinae, Tanypodinae, and oligochaete worms. Very few non-native benthic taxa were observed; hence, a separate measure of non-native benthic macroinvertebrate density was not calculated.

Three zooplankton samples were collected at each sampling station using a 30-cm-diameter, 90-cm-long, 80-µm-mesh plankton net (nine samples/site total). Zooplankton samples were collected by allowing the plankton net to sink to 0.5 m above the lake bottom and then towing it vertically through the water column (Plate 4). Plankton samples were washed from the net into a Whirl-Pak® (Nasco) sample bag using 95% EtOH. In the lab, zooplankton samples were washed through a 125 µm sieve (Newark Wire Cloth Co., Newark, New Jersey). Following washing, all zooplankton samples were diluted to a known volume of 50 ml. Sub-samples of 2.0 ml each were extracted from the 50 ml sample using a pipette, and the number of individuals in the sub-sample was determined. If there were less than 100 individuals in the first sub-sample, additional 2.0 ml sub-samples were extracted and processed until at least 100 individual zooplankton were identified across the combined sub-samples. All zooplankton were identified to the lowest practicable taxonomic level, although statistical analyses were generally based on taxonomic groups rather than individual species. Zooplankton community measures were calculated based on zooplankton total density (ZTD, number individuals/m³), dreissenid veliger density (DVD, number individuals/m³), and densities of cyclopoids, *Limnocalanus macrurus*, eucladocerans, and rotifers (number individuals/m³).

Fish communities were only sampled during summer 2003 because weather conditions precluded consistent fish sampling during summer 2004. Two methods were used to assess fish communities. Beach seines (10-m-long, 6.4-mm-mesh) were used to sample shallow water fish communities (<1.0 m water depth) during twilight

hours (i.e., 20:30 to 22:30). Three beach seine hauls (10 m long parallel to the shore) were collected at the base of each site transect (nine seine hauls/site total). Fish collected in the seines were identified to species and released after processing. Shallow water fish communities were described using catch per unit effort measures (CPU; number of individuals/beach seine haul) calculated for species occurring at three or more sites (i.e., *Fundulus diaphanous*, *Rhinichthys cataractae*, *Notropis hudsonius*, and the non-native *Alosa pseudoharengus* and *Neogobius melanostomus*), all shallow water fish combined (SWTot), planktivores (SWPlk), benthivores (SWBen), insectivores (SWIns), native fish (SWNat), and introduced fish (SWInt).

Scientific gill nets (38.0-m-long, 2.4-m-deep) were used to sample fish along the 3.0 m depth contour of study sites. The gill nets were comprised of five 7.6 m sections, each with a different mesh size (i.e., 2.5 cm, 3.8 cm, 5.1 cm, 6.4 cm, and 7.6 cm bar). Gill nets were set during twilight hours (i.e., 20:30 to 22:30) in an offshore direction with sampling station points at the shoreward end of the gill net set. Gill nets were fished for no more than four hours at a time to minimize sampling induced mortality. At the conclusion of each gill net set, the elapsed time was recorded and fish were removed from the gill net, identified to species, measured for length, and released. CPU measures (number fish captured/hr) were calculated for individual species and family groups (i.e., *Aplodinotus grunniens*, *Dorosoma cepedianum*, catostomids, salmonids, and percids), all nearshore fish combined (NSTot), piscivores (NSPis), planktivores (NSPlk), benthivores (NSBen), native fish (NSNat), and introduced fish (NSInt).

Spatial Data

Existing land cover data (IFMAP 2000) were used to map land use along the Lake Michigan shoreline. A shoreline structure data layer was also created by digitizing shore structures interpreted from digital orthophotoquads. Spatial analyses to quantify land cover and shoreline structure densities were conducted using ArcView 3.2 Geographic Information Systems (GIS, ESRI 2004) software. Land cover composition and the number of shoreline structures present at multiple scales relative to study sites were determined using buffer areas defined as 1.0 km-wide lateral bands along the shoreline. The longitudinal extent of these buffers was defined as one of five shoreline landscape contexts extending north or south from a given survey site, including local scale (a 5.0 km buffer centered on each nearshore study site), and 10 km, 25 km, 50 km, and 100 km updrift from each survey site. The direction (i.e., north or south of a given study site) of the shoreline contexts was determined based on mean longshore currents for the study area (Beletsky et al. 1999). Shoreline contexts were spatially

nested so that larger contexts encompassed the areas of all smaller contexts. The longitudinal and inland extents of each shoreline spatial context (e.g., 5.0 km long and 1.0 km inland, 10 km long and 1.0 km inland, etc.) served as the boundaries for quantifying the percentage of urban land use within buffers of each spatial context. These shoreline contexts were also used to determine the numbers of shoreline structures at multiple spatial scales relative to the study sites. Both the urban land use and shoreline structure data were used as measures of shoreline condition in regression analyses with the biological community data.

Statistical Analysis

A repeated measures analysis of variance (ANOVA) was used to determine whether benthic and zooplankton community measures were different between shoreline classes. For the ANOVAs, biological community data were $\log_{10}(x+1)$ transformed to meet the assumption of equal variance. Multivariate ANOVA (MANOVA) was used for fish data to detect potential interactions among the fish community measures relative to shoreline class. In cases where the MANOVA was significant, individual one-way ANOVAs were conducted using the fish community data to determine which groups exhibited different CPU between the shoreline classes. Regression analysis was used to determine whether overall mean local biological community measures were related to the spatial extent of urban land uses and numbers of shoreline structures within the shoreline buffers described previously. The statistical software package SPSS 12.0 (SPSS, Inc.) was used to conduct all statistical analyses. Statistical tests were significant at $\alpha = 0.05$.

RESULTS

Summary

Site surveys were primarily conducted during late June and July of 2003 (benthic macroinvertebrates, zooplankton, fish, and water chemistry) and 2004 (benthic macroinvertebrates and zooplankton) (Table 1). For each site, zooplankton and benthic samples were collected within the same 2-week time frame each year. Water temperatures, dissolved oxygen, conductivity, and pH measures were largely similar among sites (Table 2). However, Secchi depth measures varied widely among sites, ranging from 2.0 m at PP to 8.2 m at LU (Table 2). Turbidity tended to decrease in a northward direction across the study sites and likely reflected differences in the relative productivity of the nearshore areas. However, there was no statistically significant difference in Secchi depth between the shoreline classes.

Benthic samples were principally comprised of taxa in ten coarse taxonomic groups, including intermittent occurrences of the introduced species, *D. polymorpha* (Table 3). Twenty-four zooplankton taxa were observed

across all sites, including two non-native species, *Cercopagis pengoi* and *Dreissena sp. veligers* (Table 4). Twenty-three fish species were also observed among the study sites, including the introduced species *A. pseudoharengus*, *Osmerus mordax*, *N. melanostomus*, *Salmo trutta*, and *Onchorhynchus tshawytscha* (Tables 5 and 6).

Local Shoreline Type Analyses

Benthic macroinvertebrate invertebrate community compositions and densities varied widely within and among study sites (Table 3). Repeated measures ANOVA indicated that BMTD was not significantly different between shoreline types ($F=0.14$, $p=0.71$, Fig. 2a), although it was greater in 2003 vs. 2004 ($F=17.55$, $p<0.001$). Four of the 10 observed taxonomic groups occurred with sufficient frequency to warrant statistical comparisons between modified and intact shoreline classes, including the chironomid subfamilies Chironominae, Orthocladiinae, and Tanypodinae, and oligochaete worms (Table 3). Densities of Chironominae did not differ between shoreline classes ($F=0.59$, $p=0.45$), although they were higher in 2003 compared to 2004 ($F=5.17$, $p=0.03$) (Fig. 3a). Orthocladiinae densities were also not different between shoreline classes ($F=0.76$, $p=0.76$), but were higher in 2003 vs. 2004 ($F=89.85$, $p<0.001$) (Fig. 3b). Tanypodinae densities were not different between shoreline classes ($F=0.15$, $p=0.70$), although they were greater in 2004 vs. 2003 ($F=65.00$, $p<0.001$) (Fig. 3c). Finally, oligochaete worm densities were not different between shoreline classes ($F=0.65$, $p=0.42$), but were significantly higher during 2003 compared to 2004 ($F=5.49$, $p=0.02$) (Fig. 3d). The only non-native benthic invertebrate observed was *Dreissena polymorpha*, and it was only observed in very low densities at two of the eight sites (SJ and SL), thus precluding this group from statistical analysis.

Zooplankton densities were moderately variable among sites, although generally not to the same extent as benthic macroinvertebrates (Tables 3 and 4). Mean ZTD was not significantly different between shoreline classes ($F=0.07$, $p=0.80$) (Fig. 2a), although it was significantly different between 2003 and 2004 ($F=25.11$, $p<0.001$). However, a significant interaction between the year and shoreline class treatments ($F=12.15$, $p=0.001$) suggested that this pattern was not consistent between shoreline types (Fig. 2b). Mean ZTD was lower in 2003 compared to 2004 for the modified shoreline type ($F=29.17$, $p<0.001$), although there was no significant difference in mean ZTD of intact shorelines between years ($F=0.08$, $p=0.78$) (Fig. 2b).

Statistical analyses of individual zooplankton taxonomic groups were restricted to higher levels of organization in most cases due to the high degree of

Table 1. Sample dates for nearshore areas in Lake Michigan surveyed during the summers of 2003 and 2004.

Study Site	Taxonomic Group			
	Zooplankton	Benthic Invertebrates	Shallow Water Fish	Nearshore Fish
Ludington	29-Jul-03	29-Jul-03	19-Aug-03	19-Aug-03
	12-Jul-04	12-Jul-04		
Mizpah Park	24-Jun-03	24-Jun-03	24-Jun-03	24-Jun-03
	11-Jul-04	11-Jul-04		
Pioneer Park	30-Jun-03	30-Jun-03	30-Jun-03	30-Jun-03
	1-Jul-04	1-Jul-04		
Pere Marquette	30-Jul-03	30-Jul-03	29-Jul-03	29-Jul-03
	2-Jul-04	2-Jul-04		
South Holland	14-Jul-03	14-Jul-03	14-Jul-03	14-Jul-03
	3-Jul-04	3-Jul-04		
Silver Lake	29-Jul-03	29-Jul-03	29-Jul-03	29-Jul-03
	2-Jul-04	2-Jul-04		
Whitehall	1-Jul-03	1-Jul-03	01-Jul-03	01-Jul-03
	10-Jul-04	10-Jul-04		

Table 2. Mean (± 1 S.E.) physicochemical measures for nearshore areas adjacent to modified and intact shorelines of Lake Michigan. Water temperature, dissolved oxygen, conductivity, and pH measures are based on measurements taken at 2.0 m water depth along the 3.0 m depth contour of study sites.

Shoreline Class	Study Site	Physicochemical Measure				
		Secchi Depth (m)	Water Temperature ($^{\circ}$ C)	Dissolved Oxygen (mg/L)	Conductivity (μ S)	pH
Modified	Saint Joseph	3.1 \pm 0.1	19.0 \pm 0.1	9.9 \pm 0.6	362.0 \pm 81.5	8.2 \pm 0.1
	Pioneer Park	2.0 \pm 0.1	20.3 \pm 0.2	9.4 \pm 0.1	490.0 \pm 92.5	8.2 \pm 0.1
	Whitehall	4.5 \pm 0.1	21.5 \pm 0.1	8.5 \pm 0.4	497.0 \pm 97.0	8.2 \pm 0.0
	Silver Lake	6.5 \pm 0.6	19.4 \pm 0.1	9.9 \pm 0.1	528.3 \pm 0.3	8.4 \pm 0.1
Intact	Mizpah Park	4.7 \pm 0.3	20.6 \pm 0.1	10.3 \pm 0.6	668.7 \pm 2.3	8.4 \pm 0.1
	South Holland	2.2 \pm 0.0	23.4 \pm 0.3	10.6 \pm 0.3	628.3 \pm 16.8	8.5 \pm 0.0
	Pere Marquette	6.2 \pm 0.1	20.4 \pm 0.0	9.4 \pm 0.1	538.7 \pm 0.9	8.4 \pm 0.0
	Ludington	8.2 \pm 0.1	19.3 \pm 0.1	9.9 \pm 0.0	525.0 \pm 2.6	8.5 \pm 0.0

variability in densities of individual genera and/or species within and among sites, between shoreline classes, and between years (Table 4). The cyclopoid group included five taxa and tended to be numerically scarce compared to most other zooplankton groups (Table 4). Total cyclopoid densities were not different between modified and intact shorelines ($F=0.21$, $p=0.65$), although they were consistently higher in 2003 vs. 2004 for both shoreline classes ($F=26.78$, $p<0.001$) (Fig. 4a). There was no interaction between year and shoreline type for the cyclopoid analysis ($F=0.27$, $p=0.61$). Only one calanoid species was detected, *Limnocalanus macrurus*,

and it generally occurred in small numbers across all sites (Table 4). *L. macrurus* densities were similar both between shoreline classes ($F=0.01$, $p=0.92$) and between years ($F=0.103$, $p=0.75$) with no significant interaction between the main effects ($F=1.76$, $p=0.19$) (Fig. 4b). The eucladoceran group included six different taxa, although *Bosmina longirostris* was much more abundant than any of the other eucladocerans, and it was a numerically dominant taxon in zooplankton samples across all sites (Table 4). As a group, eucladoceran densities were not different between shoreline classes ($F=1.02$, $p=0.32$), although they were lower in 2003 compared to 2004

Table 3. Mean (± 1 S.E.) benthic macroinvertebrate densities (number of individuals/m²) for nearshore areas adjacent to highly modified and largely intact shorelines of Lake Michigan. Samples were collected during summers 2003 and 2004 using a Petite Ponar® grab (0.023m²). Study sites include St. Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and south of the Ludington pump storage station (LU). Taxonomic groups include the dipteran Chironomidae (sub-families Chironominae (Chiro); Orthocladiinae (Ortho); Podonominae (Podo); Prodiamesinae (Prodi); and Tanypodinae (Tanypod); and the tribe Tanytarsini (Tanytar)), the dipteran Ceratopogonidae (Cerato), oligochaete worms (Oligo), water mites (Mites), dreissenid mussels (Dreis), and all benthic macroinvertebrates (Tot_Ben).

Shoreline Class	Site	Year	Benthic Invertebrate Taxon										
			Chiro	Ortho	Podo	Prodi	Tanypod	Tanytar	Cerato	Oligo	Mites	Dreis	Tot_Ben
Modified	SJ	2003	248.4±109.7	130.4±30.3					6.2±6.2	130.4±123.3	6.2±6.2	6.1±6.1	559.0±196.6
		2004	328.5±52.3		87.0±34.8	115.8±54.2	29.0±10.2			9.7±6.4			560.4±129.9
	PP	2003	53.1±33.0	87.0±44.7						9.7±9.7			444.4±89.0
		2004	62.8±26.2				43.5±17.8			4.8±4.8			106.3±24.2
	WH	2003	628.0±139.6	58.0±19.2			19.3±19.3		4.8±4.8	96.6±70.2	4.8±4.8		874.4±228.2
		2004	4.8±4.8				29.0±16.2	14.5±10.2		4.8±4.8			53.1±22.7
	SL	2003	53.1±18.9	140.1±108.6						9.7±6.4		4.8±4.8	236.7±125.1
		2004	14.5±10.2										14.5±10.2
Intact	MP	2003	77.3±48.5	173.9±44.1						48.3±43.1	4.8±4.8		323.7±127.8
		2004	376.8±122.1	72.5±30.7	33.8±12.1					9.7±6.4			483.1±136.4
	SH	2003	91.8±28.5	33.8±15.8						43.5±28.1			173.9±39.7
		2004	87.0±50.2			9.7±9.7	33.8±20.2						130.4±65.6
	PM	2003	333.3±71.0	58.0±21.7			14.5±14.5						444.4±89.0
		2004	58.0±29.9		4.8±4.8					9.7±6.4			62.8±30.8
	LP	2003	125.0±63.3										125.0±63.3
		2004	65.2±21.7				166.7±54.3						231.9±60.1

Table 4. Mean densities (± 1 S.E.) of native and non-native zooplankton taxa observed in vertical plankton tows collected along the 3 m depth contour of nearshore waters along Lake Michigan shorelines, including Saint Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and Ludington (LU).

Origin	Taxonomic Group	Taxon	Modified Sites					Intact Sites				
			SJ	PP	WH	SL	MP	SH	PM	LU		
	Calanoida	<i>Limnocalanus macrurus</i>	6.99 \pm 2.87	85.04 \pm 29.33	39.25 \pm 13.30	84.44 \pm 15.08	20.85 \pm 5.30	44.16 \pm 11.48	61.06 \pm 14.43	8.51 \pm 1.08		
		<i>Acanthocyclops vernalis</i>				0.58 \pm 0.58		34.34 \pm 21.32				
	Cyclopoida	<i>Diatocyclops</i> sp.	2.80 \pm 2.24	3.27 \pm 3.27		1.73 \pm 1.73	3.13 \pm 1.92	11.45 \pm 8.29				
		<i>Eucyclops</i> sp.	7.48 \pm 4.62	6.54 \pm 5.07		0.58 \pm 0.58						
		<i>Mesocyclops edax</i>	8.91 \pm 4.79	49.06 \pm 21.94	67.05 \pm 20.99		32.16 \pm 7.58	11.45 \pm 4.84	7.90 \pm 4.47	0.63 \pm 0.47		
Native		<i>Tropocyclops prasinus mexicanus</i>	2.26 \pm 1.22	32.71 \pm 17.47	65.42 \pm 22.77	1.73 \pm 1.73	17.44 \pm 6.62	8.18 \pm 5.22	3.82 \pm 1.93	0.35 \pm 0.35		
	Eucladocera	<i>Bosmina longirostris</i>	3523.98 \pm 1184.67	5799.19 \pm 1287.44	2965.83 \pm 389.65	1852.54 \pm 398.18	1809.99 \pm 272.49	7437.88 \pm 811.87	1441.34 \pm 277.37	129.56 \pm 49.46		
		<i>Ceriodaphnia</i> sp.		3.27 \pm 2.24						3.62 \pm 2.79		
		<i>Chydorus</i> sp.	59.37 \pm 11.09	40.07 \pm 14.95	107.12 \pm 25.07	182.78 \pm 46.25	370.83 \pm 60.32	21.26 \pm 12.77	68.14 \pm 21.56	6.00 \pm 4.46		
		<i>Daphnia</i> sp.	9.58 \pm 5.80	6.54 \pm 3.80	11.45 \pm 5.90	2.94 \pm 1.89		22.90 \pm 8.09	5.45 \pm 3.57	0.38 \pm 0.38		
		<i>Eubosmina coregoni</i>		55.60 \pm 55.60	1.63 \pm 1.63	0.87 \pm 0.87	14.99 \pm 10.12					
		<i>Polypheumus pediculus</i>	21.03 \pm 10.32	3.27 \pm 2.24	1.64 \pm 1.64	68.11 \pm 20.17	11.45 \pm 5.39	99.76 \pm 39.83	13.63 \pm 3.86	5.34 \pm 1.53		
	Rotifera	<i>Ascomorpha</i> sp.					7.09 \pm 4.88	137.38 \pm 67.31				
		<i>Asplancha</i> sp.	160.92 \pm 65.69	322.18 \pm 62.37	225.69 \pm 33.55	63.90 \pm 17.09	367.01 \pm 56.16	544.59 \pm 176.85	31.62 \pm 11.75	55.31 \pm 28.98		
		<i>Brachionus pterodinoideus</i>		10.63 \pm 6.71	4.91 \pm 3.57		2.86 \pm 2.46	3.27 \pm 2.24				
		<i>Kellicottia longispina</i>	723.93 \pm 151.23	322.99 \pm 105.31	841.42 \pm 262.66	594.44 \pm 194.29	1202.58 \pm 486.14	379.42 \pm 206.79	386.50 \pm 101.35	28.45 \pm 6.07		
		<i>Keratella</i> sp.	85.39 \pm 16.35	89.95 \pm 26.74	137.37 \pm 39.20	92.58 \pm 28.62	148.28 \pm 31.69	261.67 \pm 184.31	60.24 \pm 30.66	0.45 \pm 0.45		
		<i>Monostyla</i> sp.		1.64 \pm 1.64			1.64 \pm 1.64	8.18 \pm 8.18				
		<i>Ploesoma hudsonii</i>	62.15 \pm 12.76	181.53 \pm 58.80	123.47 \pm 37.25	476.77 \pm 177.72	229.23 \pm 54.97	73.59 \pm 22.73	83.95 \pm 34.60	4.30 \pm 2.32		
		<i>Polysartha</i> sp.	57.60 \pm 15.53	278.02 \pm 139.95	65.42 \pm 15.34	41.33 \pm 11.48	217.78 \pm 39.11	513.52 \pm 227.65	11.18 \pm 5.77			
Non-Native		<i>Rotifer colony</i>	30.14 \pm 11.18	13.08 \pm 6.40	149.64 \pm 67.21	49.87 \pm 17.09	39.25 \pm 19.25	577.30 \pm 175.29	20.72 \pm 8.70	0.82 \pm 0.49		
		<i>Trichocerca</i> sp.	23.97 \pm 6.52	52.33 \pm 19.56	121.02 \pm 31.04	13.45 \pm 5.41	47.15 \pm 19.25	3.27 \pm 2.24	5.72 \pm 4.15			
		<i>Cercopagis pengoi</i>	2.80 \pm 2.24	6.54 \pm 5.08	29.44 \pm 26.04	5.19 \pm 3.77		4.91 \pm 2.66	2.73 \pm 1.27			
		<i>Dreissena</i> sp. (Veliger)	445.89 \pm 151.52	191.34 \pm 40.96	811.98 \pm 212.65	279.54 \pm 79.01	3958.07 \pm 1335.52	959.17 \pm 297.85	123.75 \pm 24.25	7.12 \pm 1.87		
		Number of Taxa/Site	18	20	18	19	19	21	16	14		

Table 5. Mean (± 1 SE) catch per unit effort (CPU) measures for fish species observed in beach seines during surveys of shallow water fish communities associated with Great Lakes shoreline areas. Study sites include St. Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and south of the Ludington pump storage station (LU).

Site	Shallow Water Species (Beach Seine)										
	Alewife	Banded Killifish	Bluegill	Emerald Shiner	Johnny Darter	Juvenile Salmonid	Longnose Dace	Rainbow Smelt	Round Goby	Spottail Shiner	White Sucker
LU							1.11 \pm 1.45			1.56 \pm 3.43	
MZ		0.22 \pm 0.67			0.22 \pm 0.67		2.89 \pm 3.48		4.44 \pm 4.45	16.44 \pm 25.59	
PI	4.22 \pm 4.29	2.22 \pm 4.52		1.33 \pm 1.73		0.44 \pm 0.88				5.78 \pm 2.91	
PM		0.89 \pm 2.03								0.67 \pm 1.00	
SH	0.67 \pm 1.00	0.22 \pm 0.67							0.89 \pm 1.05	11.78 \pm 12.27	
SJ	0.22 \pm 0.67	3.11 \pm 7.15				0.89 \pm 1.45	1.33 \pm 2.83		5.33 \pm 7.55	39.78 \pm 42.57	0.22 \pm 0.67
SL	0.22 \pm 0.67									1.89 \pm 2.26	0.89 \pm 1.45
WH		1.11 \pm 1.45	0.22 \pm 0.67	0.44 \pm 0.88				0.89 \pm 1.76		3.78 \pm 2.33	

Table 6. Mean (± 1 SE) catch per unit effort (CPU) measures for fish species observed in gill nets during surveys of nearshore fish communities associated with eight Great Lakes shoreline areas. Study sites include St. Joseph (SJ), Pioneer Park (PP), Whitehall (WH), Silver Lake (SL), Mizpah Park (MP), South Holland (SH), Pere Marquette (PM), and south of the Ludington pump storage station (LU).

Site	Nearshore Species (Gill Net)										
	Brown Trout	Chinook Salmon	Freshwater Drum	Gizzard Shad	Golden Redhorse	Longnose Sucker	River Redhorse	Round Whitefish	Silver Redhorse	Walleye	White Sucker
LU	0.22 \pm 0.19	0.11 \pm 0.18	0.74 \pm 0.79		0.41 \pm 0.28	0.59 \pm 0.40			0.11 \pm 0.18	0.11 \pm 0.18	
MZ	0.08 \pm 0.14	0.08 \pm 0.14	0.08 \pm 0.14	0.09 \pm 0.15		0.17 \pm 0.15	0.09 \pm 0.15				0.33 \pm 0.37
PI			0.09 \pm 0.15								0.52 \pm 0.26
PM			0.15 \pm 0.13					0.07 \pm 0.13			
SH			1.40 \pm 0.64	0.69 \pm 0.49					0.28 \pm 0.29	0.09 \pm 0.15	0.10 \pm 0.18
SJ		0.16 \pm 0.27		0.08 \pm 0.14		0.18 \pm 0.31					1.53 \pm 0.93
SL			0.14 \pm 0.25								
WH			1.74 \pm 0.80						0.08 \pm 0.14	0.19 \pm 0.17	

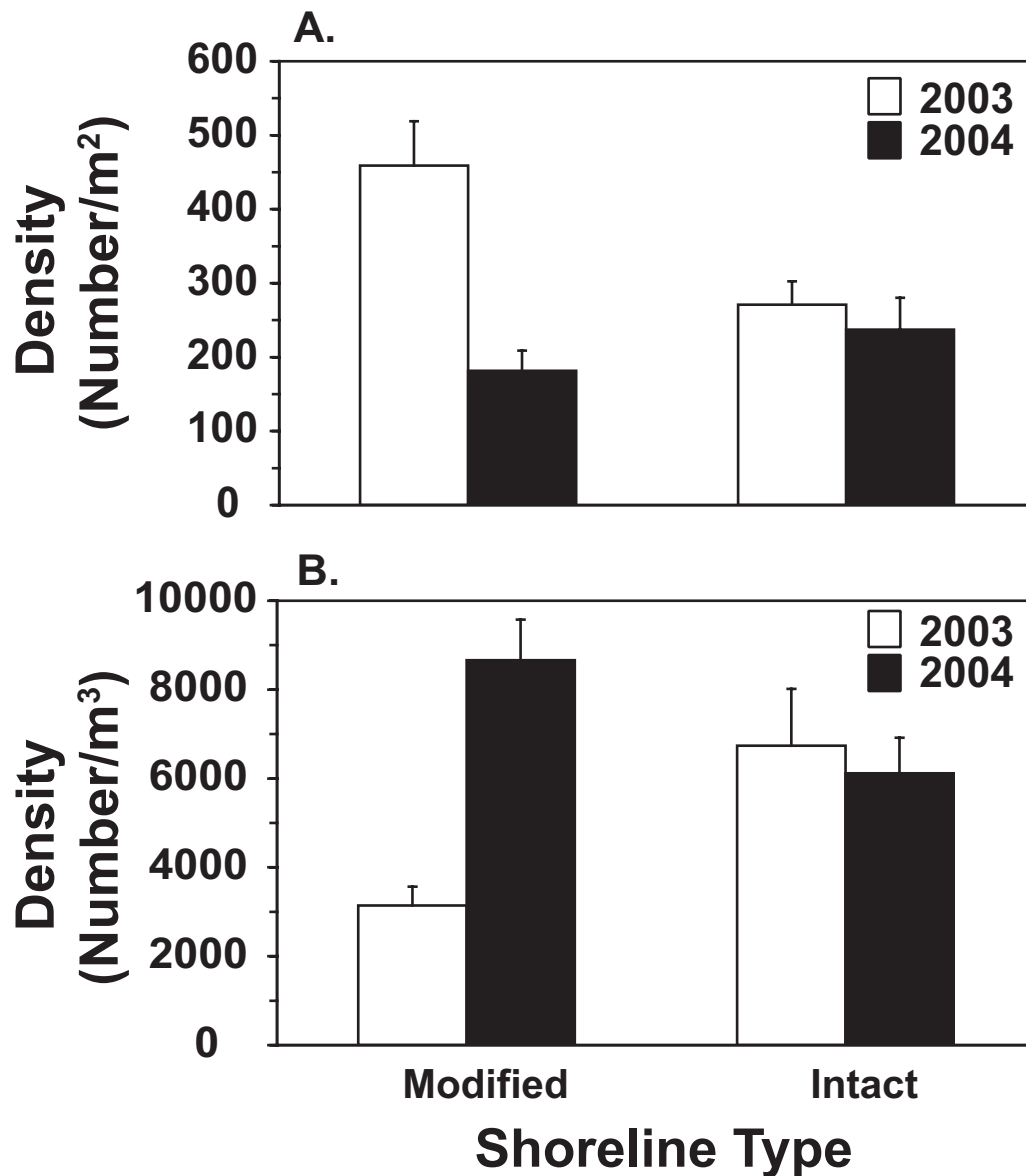


Figure 2. Mean (± 1 S.E.) total densities of A) benthic macroinvertebrates (number of individuals/m²) and B) zooplankton (number of individuals/m³) segregated by shoreline type (modified and intact) for samples collected along the 3 m depth contour of eastern Lake Michigan during summer 2003 and 2004.

($F=56.16$, $p<0.001$) (Fig. 4c). There was a nearly significant interaction between year and shoreline type due to the comparably lower degree of variability in mean eucladocern densities between 2003 and 2004 for the intact shoreline class ($F=3.06$, $p=0.09$) (Figure 4c).

Rotifers also comprised a large portion of zooplankton samples, including seven taxa that were widely distributed among the sites and three additional taxa that were only found at a few sites (Table 4). A significant interaction between year and shoreline type ($F=8.56$, $p=0.005$) indicated that ANOVAs had to be segregated by year. Rotifer densities were significantly greater in 2004 vs. 2003 for the modified shoreline class ($F=17.99$, $p<0.001$), although they were not significantly different between years for the intact shoreline class ($F=0.02$, $p=0.89$) (Fig. 4d). Overall rotifer densities were

also not significantly different between nearshore areas associated with modified vs. intact shorelines (ANOVA $F=0.07$, $p=0.80$) (Fig. 4d).

Non-native zooplankters were represented by *C. pengoi* and *Dreissena sp.* veligers. Very few *C. pengoi* were detected at sites (Table 4), and there was no significant difference in densities of *C. pengoi* between shoreline classes ($F=1.51$, $p=0.22$) or between years ($F=1.91$, $p=0.17$). There was also no significant interaction between year and shoreline class for this analysis ($F=2.86$, $p=0.1$). Veligers often comprised very large portions of zooplankton samples (Table 4). A significant interaction between year and shoreline type ($F=5.75$, $p=0.02$) indicated that ANOVAs had to be conducted separately by year. Nearshore areas adjacent to modified shorelines had greater densities of veligers

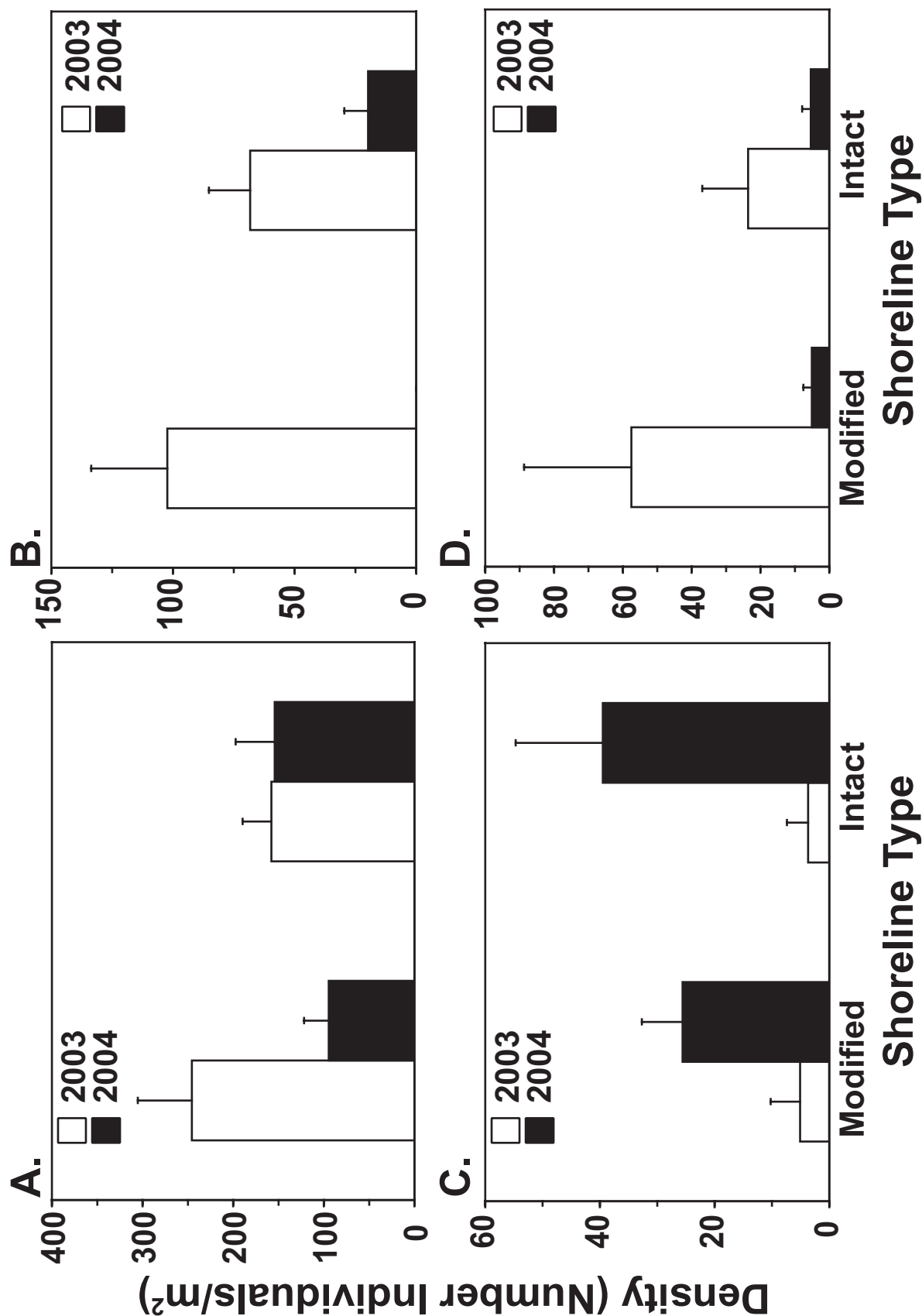


Figure 3. Mean (± 1 S.E.) densities of benthic macroinvertebrate taxonomic groups segregated by shoreline type (modified and intact) for samples collected along the 3m depth contour of eastern Lake Michigan during summer 2003 and 2004. Taxonomic groups include the chironomid subfamilies Chironominae (A), the Orthocladinae (B), and Tanypodinae (C) and oligochaete worms (D).

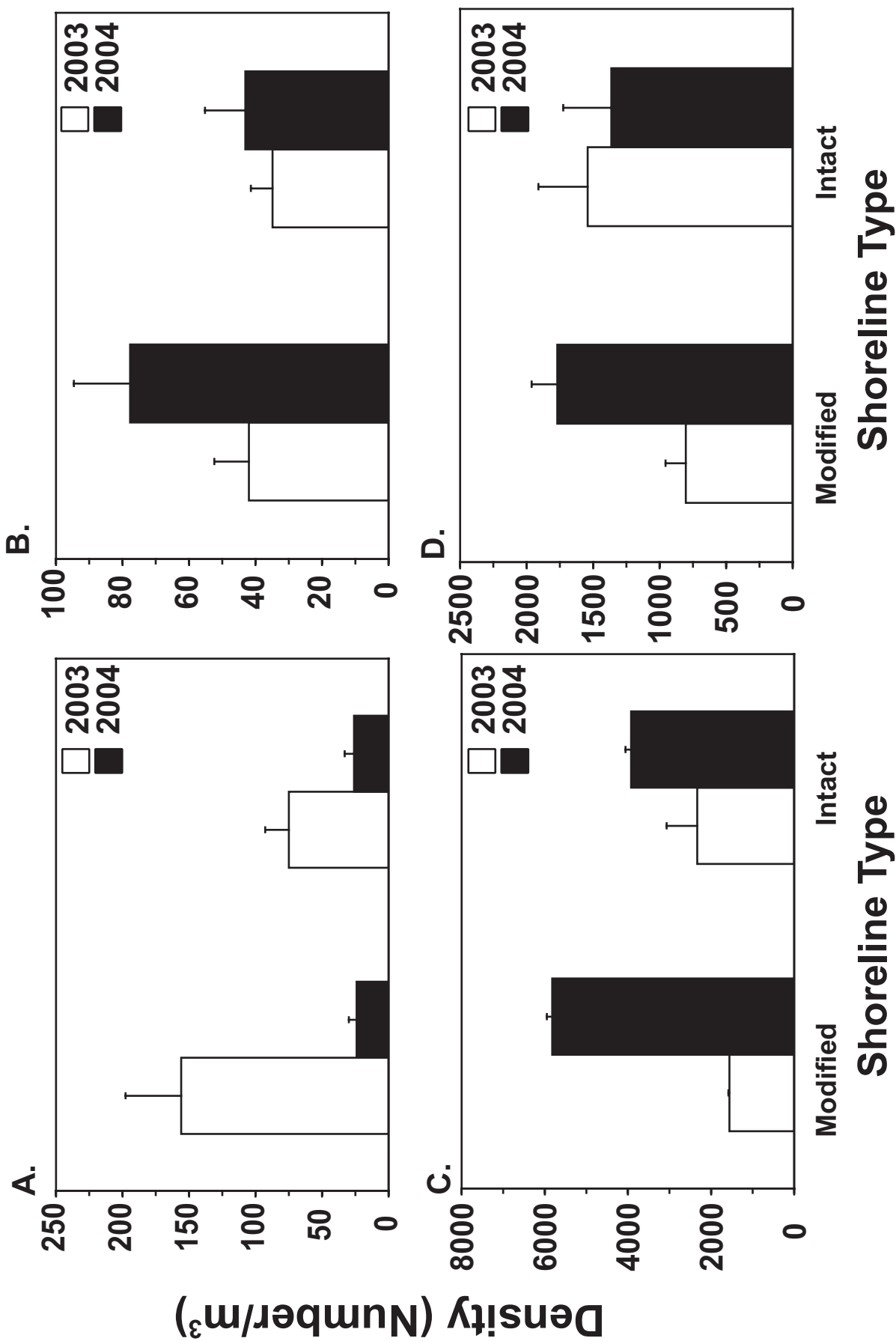


Figure 4. Mean (± 1 S.E.) densities of zooplankton taxonomic groups segregated by shoreline type (modified and intact) for samples collected along the 3 m depth contour of eastern Lake Michigan during summer 2003 and 2004. Taxonomic groups include Cyclopoida (A), Cladocera (B), Rotifera (C) and

in 2004 compared to 2003 ($F=8.51$, $p=0.005$), although this was not the case for nearshore areas along intact shorelines ($F=0.01$, $p=0.97$). There was no difference in veliger densities between shoreline types ($F=0.08$, $p=0.79$).

Most shallow water fish were only found at three or fewer sites (Table 5). The most common fish observed among sites were *N. hudsonius*, *A. pseudoharengus*, and *F. diaphanus* (Table 5). A MANOVA conducted using data for all shallow water fish species at three or more sites indicated that the shallow water fish community varied between modified and intact shoreline types ($\tilde{\epsilon}=0.83$, $p=0.03$). Individual ANOVAs for each of these fish species indicated that *A. pseudoharengus* ($F=2.43$, $p=0.12$), *R. cataractae* ($F=2.33$, $p=0.13$), *N. melanostomus* ($F=0.00$, $p=1.00$), and *N. hudsonius* ($F=1.18$, $p=0.28$) CPU measures were not significantly different between the shoreline types (Fig. 5a). This was also true for SWTot ($F=0.77$, $p=0.39$) (Fig. 5a). Only *F. diaphanus* CPU was different between shoreline types, with greater CPU in nearshore areas adjacent to modified shorelines ($F=0.77$, $p=0.39$) (Fig. 5a).

MANOVA indicated an overall difference in shallow water fish mean CPU between shoreline types based on trophic classifications ($\tilde{\epsilon}=0.83$, $p=0.03$). Mean SWPis and SWPlk were greater in nearshore areas adjacent to modified shorelines ($F=5.06$, $p=0.03$, and $F=3.88$, $p=0.05$, respectively) (Fig. 5b). Both SWBen and SWIns mean CPU were similar between the shoreline types ($F=0.35$, $p=0.56$ and $F=1.26$, $p=0.27$, respectively) (Fig. 5b). Mean SWNat and SWInt were not significantly different between shoreline types ($F=1.66$, $p=0.20$ and $F=1.68$, $p=0.20$, respectively) (Fig. 5c).

All but one nearshore fish species (*A. grunniens*) occurred at three or fewer sites (Table 6). Thus, all species but *A. grunniens* and *D. cepedianum* were grouped into family groups for analysis (i.e., catostomids, salmonids, and percids). A MANOVA indicated that nearshore fish exhibited no differences in CPU between shoreline classes based on these taxonomic groupings ($\tilde{\epsilon}=0.73$, $p=0.29$) (Fig. 6a). A MANOVA conducted using the nearshore fish data grouped according to species' trophic status indicated no overall difference in the nearshore fish community between shoreline types based on trophic status ($\tilde{\epsilon}=0.86$, $p=0.39$) (Fig. 6b). Both NSNat ($F=0.01$, $p=0.93$) and NSInt ($F=1.37$, $p=0.25$) were also not significantly different between shoreline types (Fig. 6c).

Spatial Analysis Results

Urban land uses were a prominent feature of the shoreline buffers over almost all landscape contexts (Table 7). The lowest percentages of urban land use occurred in buffers of the local and 10 km updrift landscape contexts for the SH study site (9% and 8%,

respectively), while the greatest percentage of urban land use occurred within the local landscape context at SJ (83%). The variability in urban land use within multi-scale buffers was judged to provide an appropriate basis for conducting regression analyses to detect relationships between biological community measures and urban land use of buffers quantified over multiple spatial scales.

Shore structures were also very prominent features of the buffers defined at different scales (Table 8). The number of shore structures generally increased with increasing spatial scale of landscape contexts for each study site. Shore structures ranged in number from none in the local landscape context at PP to 461 in the buffer comprising the largest landscape context for the same site. As was the case for the urban land use analyses, the variability in the number of shore structures over multiple landscape contexts for each site was judged to provide an adequate basis for conducting regression analyses to detect relationships between biological community measures and the number of shore structures within buffers of landscape contexts over multiple spatial scales.

Regression analyses of benthic community data with urban land use and shore structure density were limited to mean BMTD and CTD. The greatest variability in BMTD was explained by the extent of urban land uses within 1.0 km shoreline buffers of the local, 10 km updrift, and 25 km updrift landscape contexts (Table 9). Although these relationships were not statistically significant, the degree of variability in mean BMTD explained by urban land use dropped precipitously at the 50 km and 100 km updrift landscape contexts (Table 9). Urban land use of shoreline buffers over all landscape contexts explained very little of the variation in mean CTD (Table 9). Variability in CTD explained by urban land use was limited to a maximum of 13% observed for the 100 km updrift landscape context.

Shore structures of the two largest landscape contexts explained the greatest degree of variation in mean BMTD (Table 10). There was a nearly significant relationship between BMTD and the number of shoreline structures within the 50 km updrift landscape context ($R^2=0.45$, $p=0.07$), and the degree of variation explained by the number of structures within the 100 km updrift landscape context, though not statistically significant, was much greater than the three smallest landscape contexts (Table 10). The number of shore structures within shoreline buffers explained <5% of the variation in mean CTD over all landscape contexts (Table 10).

The extent of urban land use within the shoreline buffers explained very little variability in the ZTD dataset (Table 9). The coefficients of determination for these analyses were generally $R^2<0.07$, and the greatest variability in mean ZTD explained by urban land use was limited to 12% for the 100 km updrift landscape

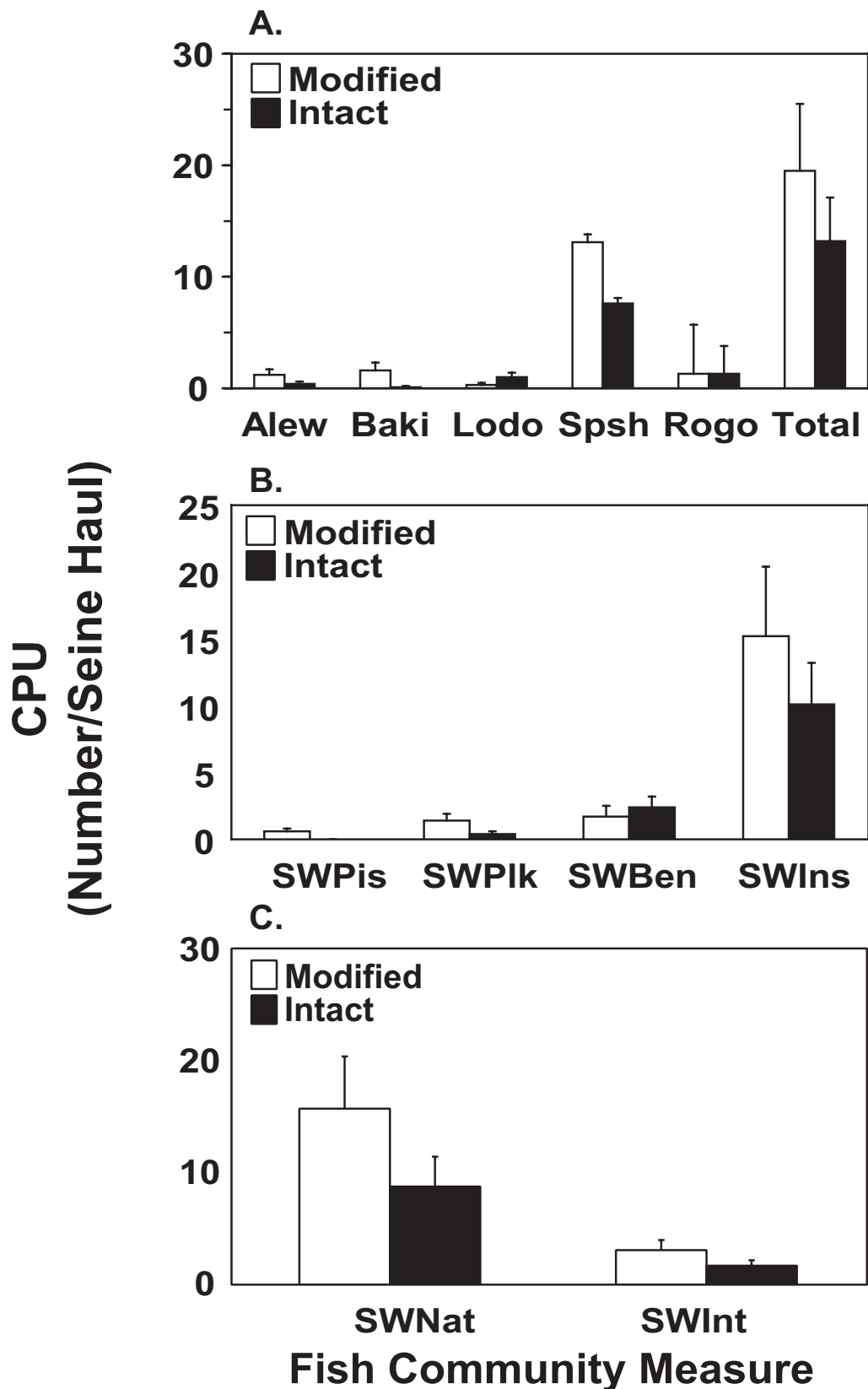


Figure 5. Mean (± 1 S.E.) catch per unit effort (CPU) for shallow water fish captured in beach seine hauls at sites segregated by shoreline type (modified and intact) in eastern Lake Michigan during summer 2003. Individual species at >3 study sites include *Alosa pseudoharengus* (alewife, Alew), *Fundulus diaphanus* (banded killifish, Baki), *Rhinichthys cataractae* (longnose dace, Lodo), and *Neogobius melanostomus* (round goby, Rogo). Groupings include overall shallow water piscivores (SWPis), planktivores (SWPlk), benthivores (SWBen), insectivores (SWIns), native fish (SWNat) and introduced fish (SWInt).

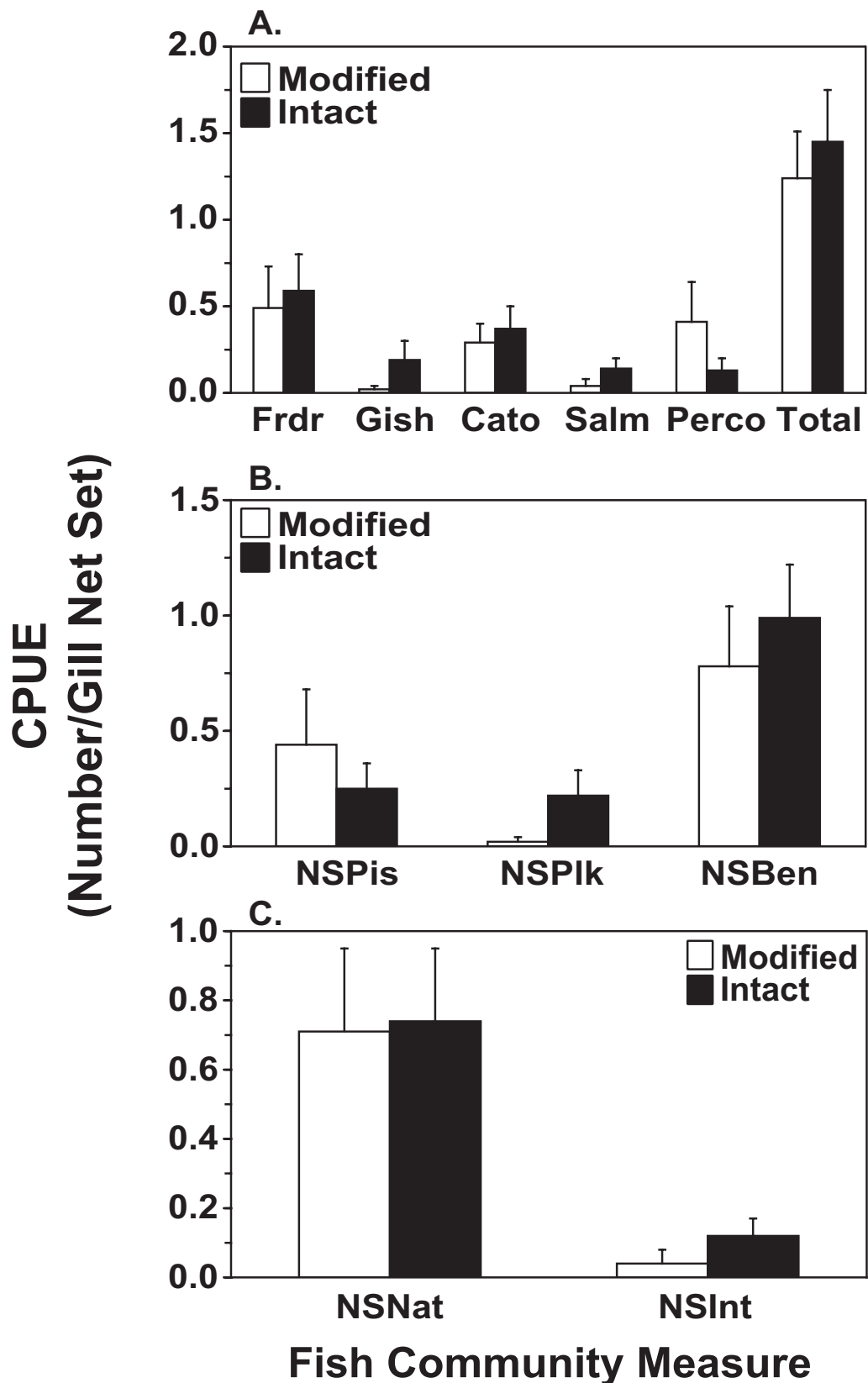


Figure 6. Mean (± 1 S.E.) catch per unit effort (CPU) for nearshore fish captured in gill net hauls at sites segregated by shoreline type (modified and intact) in eastern Lake Michigan during summer 2003. Individual species and families at >3 study sites include *Aplodinotus grunniens* (freshwater drum, Frdr), *Dorosoma cepedianum* (gizzard shad, Gish), catostomids (Cato), salmonids (Salm), and percids (Perco). Groupings include overall nearshore piscivores (SWPis), planktivores (SWPIk), benthivores (SWBen), native fish (SWNat) and introduced fish (SWInt).

Table 7. Percentage of 1.0 km shoreline buffers comprised of urban land uses along the eastern Lake Michigan shoreline. Buffers include a 5 km-long shoreline reach encompassing each study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shoreline reaches updrift from each study site.

Study Site	Buffer Landscape Context				
	Local	10 km	25 km	50 km	100 km
Saint Joseph	83	81	46	34	35
Pioneer Park	48	51	48	45	43
Whitehall	28	29	35	40	42
Silver Lake	21	15	20	25	35
Mizpah Park	19	24	41	28	28
South Holland	9	8	20	26	26
Pere Marquette	32	20	18	23	33
Ludington	26	29	33	26	34

context (Table 9). Urban land use within shoreline buffers also explained very little of the variation in DVD over most landscape contexts (Table 9). Similar to ZTD regressions, the greatest amount of variability in DVD was explained by the extent of urban land use within the largest landscape context ($R^2=0.26$, $p=0.20$).

Shore structures within shoreline buffers explained relatively little of the variation in ZTD over all landscape contexts (Table 10). The local shoreline context explained the greatest degree of variability in ZTD ($R^2=0.18$), and the remaining landscape contexts explained <3% of the variation in ZTD (Table 10). Shore structures within the three smallest landscape contexts explained <5% of the variation in DVD for each analysis, and numbers of shore structures within the two largest landscape contexts explained comparatively much larger degrees of variation, although neither was statistically significant (Table 10).

Mean SWTot was positively related to the spatial extent of urban land uses within the 10 km updrift landscape context (Fig. 7a). It also exhibited a nearly significant relationship to urban land uses of the local landscape context (Table 9). Urban land use within the two largest spatial contexts explained very little of the variation in SWTot (Table 9). In contrast, mean SWTot showed a significant negative relationship with the number of shore structures within the 100 km updrift landscape context (Fig. 8a).

Relationships between shallow fish trophic groups and urban land uses varied greatly based on landscape context, while relationships between these groups and shore structures of shoreline buffers were more similar. Mean SWIns was positively related to urban land use within buffers of the local and 10 km updrift landscape contexts (Table 9). Mean SWPlk was positively related to urban land use within the 50 km updrift landscape context (Table 9 and Fig. 7b). Mean SWBen was not

Table 8. Number of shore structures within 1.0 km shoreline buffers along the eastern Lake Michigan shoreline. Buffers include a 5 km-long shoreline reach encompassing each study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shoreline reaches updrift from each study site.

Study Site	Buffer Landscape Context				
	Local	10 km	25 km	50 km	100 km
Saint Joseph	47	96	111	129	129
Pioneer Park	0	90	123	209	461
Whitehall	7	19	93	155	420
Silver Lake	51	48	120	234	396
Mizpah Park	20	38	107	126	126
South Holland	1	4	66	173	300
Pere Marquette	23	47	117	229	346
Ludington	13	20	46	140	279

significantly related to urban land uses of any landscape context, although the smaller landscape contexts explained more variability in SWBen than the largest two landscape contexts (Table 9). In contrast, both SWIns and SWBen were negatively related to the number of shore structures in the 100 km updrift landscape context (Fig. 9a-b). Similarly, although SWPlk was not significantly related to the number of shore structures within any landscape context, the greatest amount of variation in SWPlk was explained by the number of shore structures within the 100 km updrift context (Table 9).

Mean SWNat exhibited significant positive relationships with the spatial extent of urban land use in local and 10 km updrift buffers (Table 9 and Fig. 7c). In contrast, mean SWNat was negatively related to the number of shoreline structures within the largest buffer context (Table 10 and Fig. 9c). Regression analysis showed that SWInt was positively related to urban land use of the local, 10 km updrift, and 25 km updrift buffer contexts (Table 9 and Fig. 7d). Mean SWInt also showed a significant positive relationship with the number of shore structures in the 10 km updrift buffer context (Table 10 and Fig. 9d).

Urban land uses within shoreline buffers explained very little of the variation in mean NSTot (Table 9). Although not statistically significant, urban land use within the largest spatial context explained the greatest degree of variation in NSTot (Table 9). Mean NSTot showed a significant negative relationship with the number of shore structures within the 50 km updrift landscape context (Table 10 and Fig. 8b). Shore structures within the remaining buffer contexts explained <28% of the variation in NSTot (Table 10).

Mean NSPis was positively related to urban land uses of the local and 10 km updrift landscape contexts (Fig. 11a), and urban land use of the two largest buffer contexts accounted for very little variation in mean NSPis

Table 9. Results of linear regressions between biological community measures and the spatial extent of urban land use (i.e., % buffer area as urban) within 1-km shoreline buffers defined at multiple spatial scales. Buffers included a 5 km shoreline encompassing the study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shorelines updrift from the study sites. Biological community measures are defined in the Methods section of the text. Statistically significant relationships between biological community parameters and the number of shore structures within a given buffer context are highlighted in gray.

Taxonomic Group	Community Measure	Landscape Context											
		Local			10			25			50		
		R ²	F	p	R ²	F	p	R ²	F	p	R ²	F	p
Zooplankton	ZTD	0.05	0.32	0.59	0.02	0.12	0.74	0.02	0.15	0.72	0.06	0.37	0.57
	DVD	0.09	0.62	0.46	0.04	0.23	0.65	0.05	0.33	0.59	0.01	0.07	0.80
Benthic Macroinvertebrates	BMTD	0.30	2.61	0.16	0.34	3.04	0.13	0.26	2.07	0.20	0.07	0.46	0.52
	CTD	0.06	0.36	0.57	0.04	0.22	0.65	0.00	0.01	0.95	0.07	0.47	0.52
Shallow Water Fish	SWTot	0.47	5.29	0.06	0.53	6.65	0.04	0.36	3.33	0.12	0.03	0.18	0.69
	SWPlk	0.04	0.28	0.62	0.08	0.52	0.50	0.24	1.90	0.22	0.63	10.19	0.02
	SWBen	0.15	1.09	0.34	0.22	1.66	0.25	0.27	2.20	0.19	0.00	0.02	0.90
	SWIns	0.50	6.06	0.05	0.56	7.53	0.03	0.34	3.09	0.13	0.04	0.23	0.65
	SWInt	0.51	6.23	0.05	0.60	8.99	0.02	0.61	9.45	0.02	0.23	1.81	0.23
	SWNat	0.54	7.06	0.04	0.59	8.70	0.03	0.34	3.14	0.13	0.05	0.30	0.60
Nearshore Fish	NSTot	0.00	0.00	0.99	0.02	0.09	0.77	0.07	0.47	0.52	0.04	0.23	0.65
	NSPis	0.59	8.46	0.03	0.62	9.80	0.02	0.28	2.29	0.18	0.01	0.03	0.86
	NSPlk	0.14	0.97	0.36	0.14	1.01	0.36	0.15	1.08	0.34	0.10	0.70	0.44
	NSBen	0.24	1.87	0.22	0.12	0.83	0.40	0.00	0.01	0.92	0.08	0.50	0.51
	NSNat	0.18	1.27	0.30	0.25	1.99	0.21	0.28	2.35	0.18	0.03	0.17	0.70
	NSInt	0.03	0.18	0.69	0.08	0.51	0.50	0.12	0.81	0.40	0.21	0.28	0.61

Table 10. Results of linear regressions between biological community measures and the number of shoreline structures (i.e., revetments, jetties, groin fields, etc.) within 1-km shoreline buffers defined at multiple spatial scales. Buffers included a 5 km shoreline encompassing the study site (local), and 10 km-, 25 km-, 50 km-, and 100 km-long shorelines updrift from the study sites. Biological community measures are defined in the Methods section of the text. Statistically significant relationships between biological community parameters and the number of shore structures within a given buffer context are highlighted in gray.

Taxonomic Group	Community Measure	Landscape Context											
		5			10			25			50		
		R ²	F	p	R ²	F	p	R ²	F	p	R ²	F	p
Zooplankton	ZTD	0.18	1.28	0.30	0.01	0.07	0.79	0.01	0.05	0.83	0.02	0.15	0.71
	DVD	0.01	0.04	0.85	0.04	0.24	0.64	0.01	0.04	0.86	0.24	1.91	0.22
Benthic Macroinvertebrates	BMTD	0.07	0.45	0.53	0.06	0.41	0.55	0.03	0.18	0.69	0.45	4.83	0.07
	CTD	0.01	0.07	0.81	0.02	0.09	0.77	0.00	0.00	0.96	0.04	0.25	0.64
Shallow Water Fish	SWTot	0.14	0.99	0.36	0.31	2.67	0.15	0.05	0.32	0.60	0.36	3.33	0.12
	SWPlk	0.26	2.08	0.20	0.20	1.46	0.27	0.10	0.63	0.46	0.09	0.57	0.48
	SWBen	0.13	0.87	0.39	0.09	0.62	0.46	0.01	0.08	0.78	0.52	6.39	0.05
	SWIns	0.15	1.02	0.35	0.28	2.35	0.18	0.03	0.20	0.67	0.38	3.65	0.11
	SWInt	0.02	0.11	0.76	0.55	7.34	0.04	0.20	1.45	0.27	0.16	1.16	0.32
	SWNat	0.14	1.00	0.36	0.30	2.57	0.16	0.03	0.20	0.67	0.36	3.35	0.12
Nearshore Fish	NSTot	0.16	1.12	0.33	0.11	0.74	0.42	0.27	2.22	0.19	0.54	7.14	0.04
	NSPis	0.25	1.95	0.21	0.24	1.89	0.22	0.00	0.00	0.98	0.43	4.52	0.08
	NSPlk	0.12	0.79	0.41	0.21	1.59	0.25	0.17	1.20	0.32	0.01	0.03	0.87
	NSBen	0.58	8.42	0.03	0.41	4.23	0.09	0.26	2.12	0.20	0.13	0.93	0.37
	NSNat	0.00	0.01	0.94	0.11	0.72	0.43	0.00	0.01	0.93	0.37	3.59	0.11
	NSInt	0.01	0.08	0.79	0.00	0.01	0.93	0.30	2.61	0.16	0.48	5.58	0.06

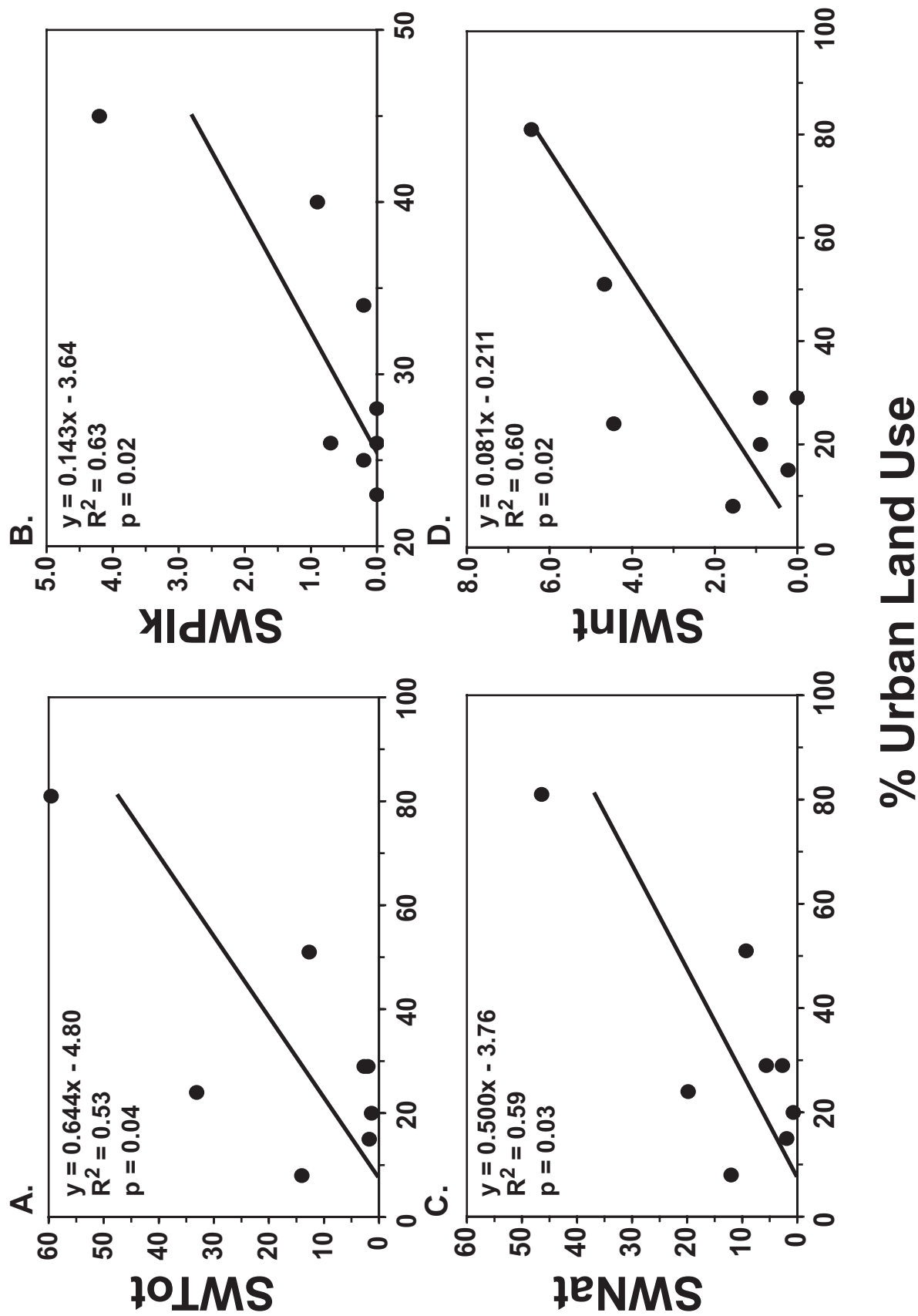


Figure 7. Relationships between A) total shallow water fish catch per unit effort (SWTot) and urban land use within the 10 km updrift landscape context, B) shallow water planktivorous fish CPU (SWPlk) and urban land use within the 50 km updrift landscape context, C) shallow water native fish CPU (SWNat) and urban land use within the 10 km updrift landscape context, and D) shallow water introduced species CPU (SWInt) and urban land use within the 10 km updrift landscape context.

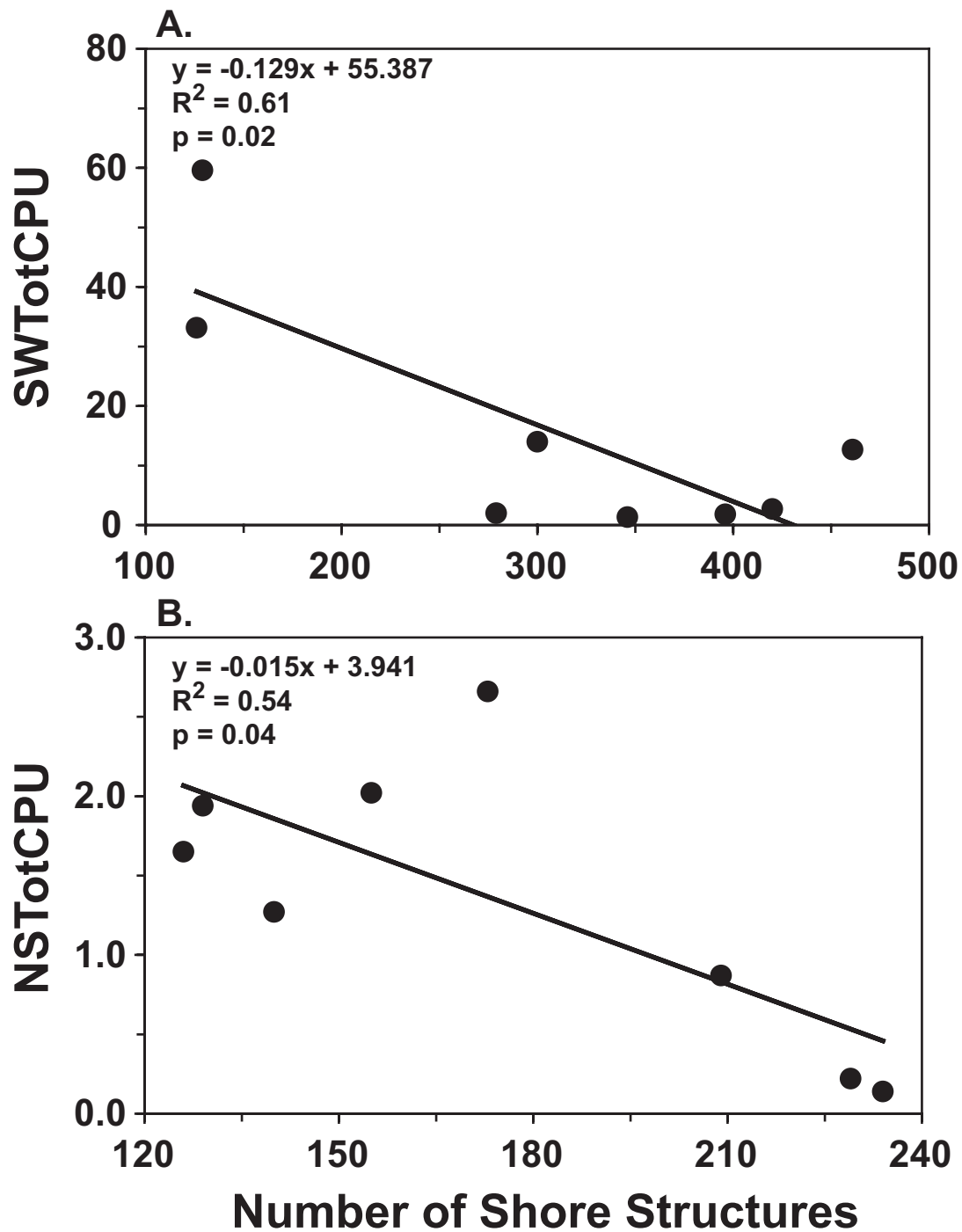
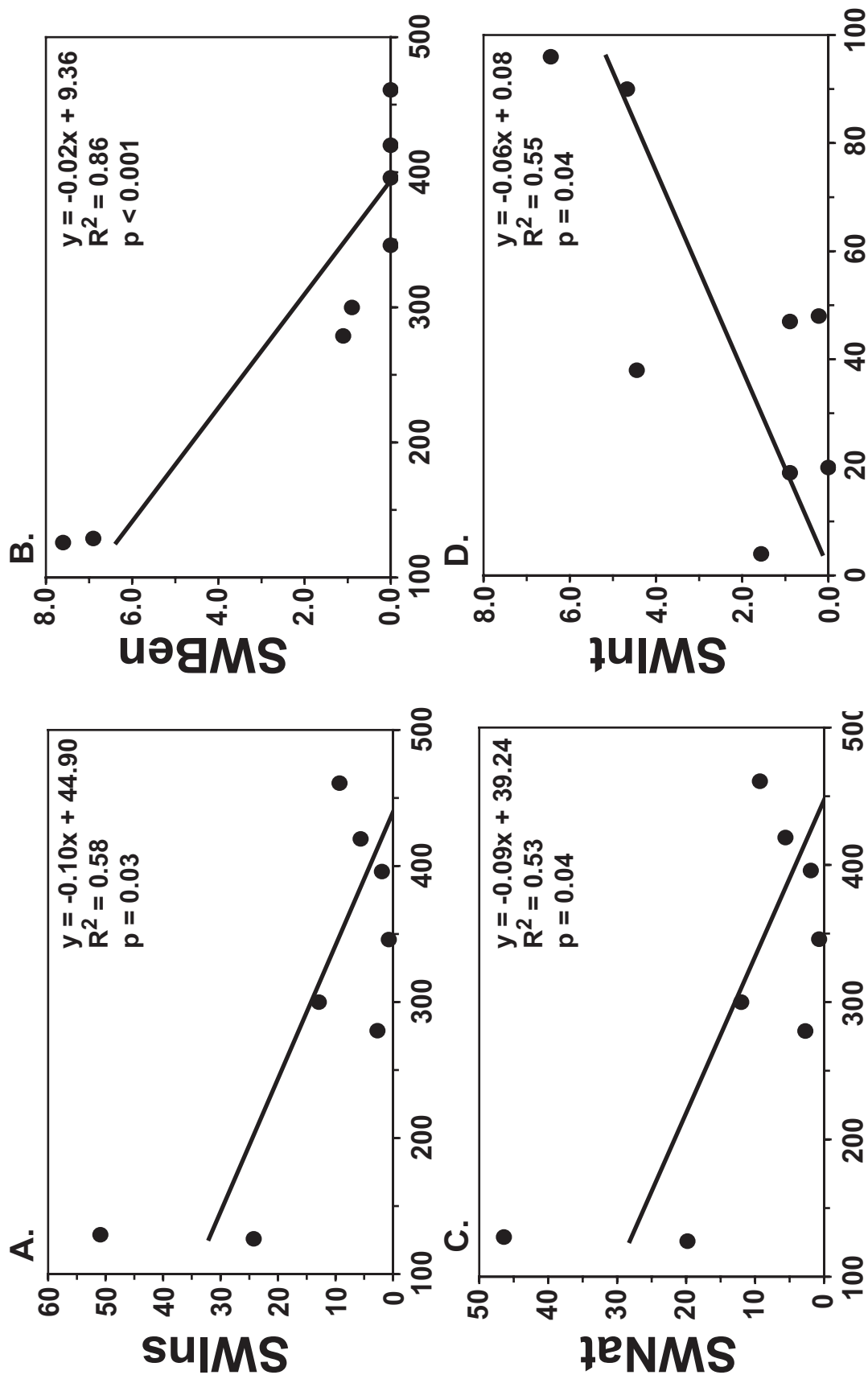


Figure 8. Relationships between A) total shallow water fish catch per unit effort (SWTot) and the number of shore structures within the 100 km updrift landscape context, and B) total nearshore fish catch per unit effort and the number of shore structures within the 50 km updrift landscape context.



Number of Shore Structures

Figure 9. Relationships between A) shallow water insectivorous fish catch per unit effort (SWIns) and the number of shore structures within the 100 km updrift landscape context, B) shallow water benthivorous fish CPU (SWBen) and the number of shore structures within the 100 km updrift landscape context, C) shallow water native fish CPU (SWNat) and the number of shore structures within the 100 km updrift landscape context, and D) shallow water introduced species CPU (SWInt) and the number of shoreline structures within the 10 km updrift landscape context.

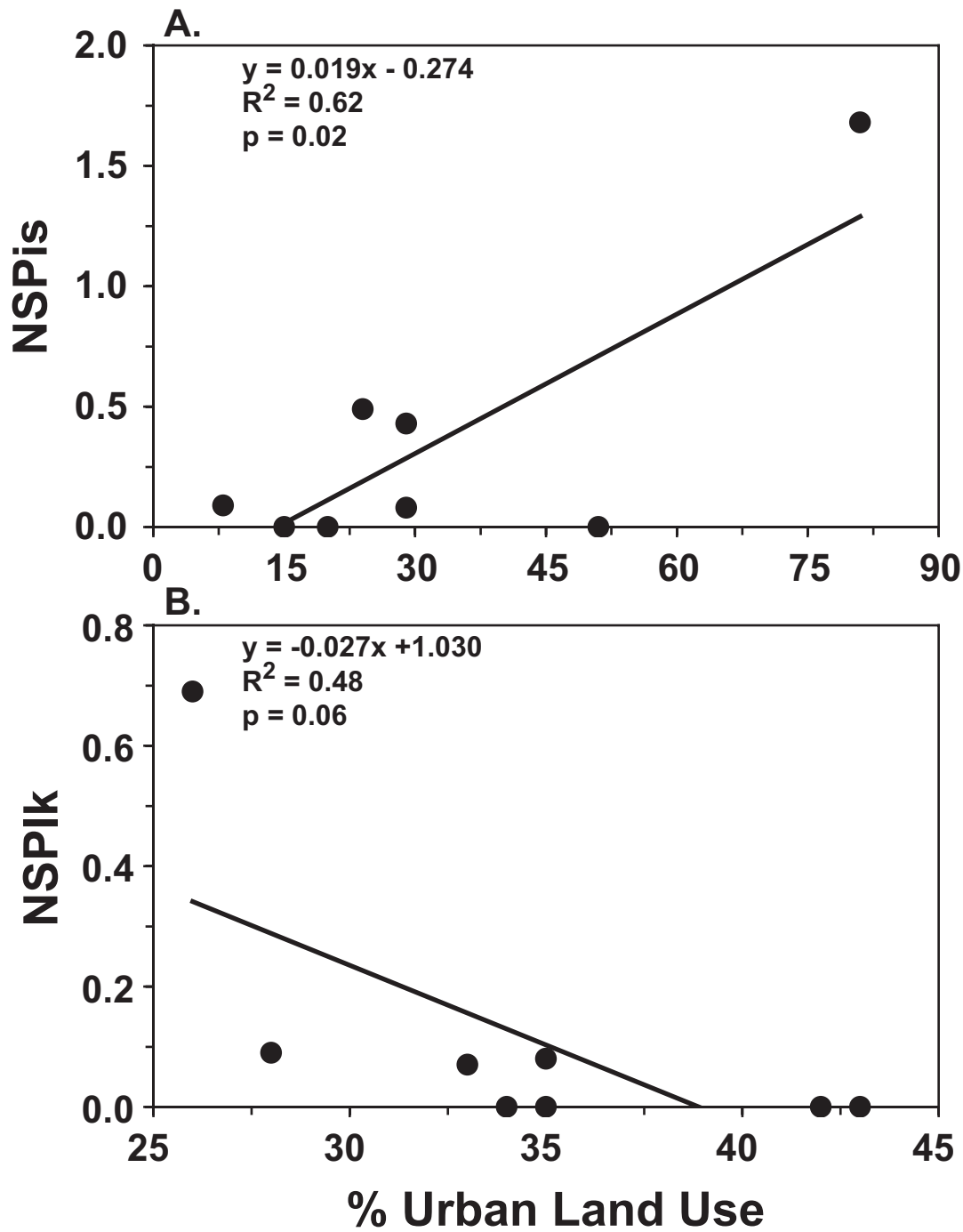
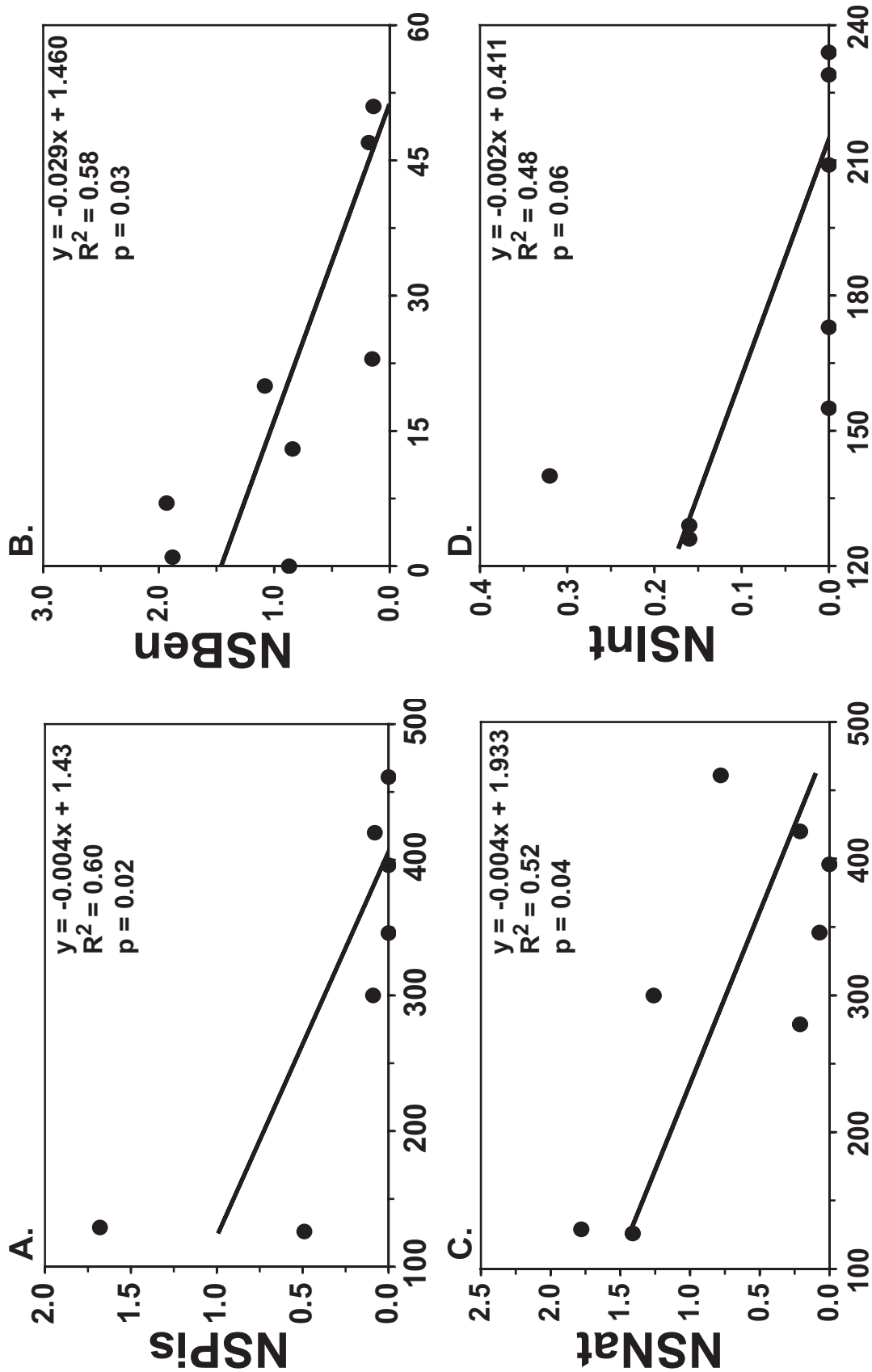


Figure 10. Relationships between A) nearshore piscivorous fish catch per unit effort (NSPis) and urban landuse within the 10 km updrift landscape context, and B) nearshore planktivorous fish catch per unit effort and urban land use within the 100 km updrift landscape context.



Number of Shore Structures

Figure 11. Relationships between A) nearshore piscivorous fish catch per unit effort (NSPis) and the number of shore structures within the 100 km updrift landscape context, B) nearshore benthivorous fish CPU (NSBen) and the number of shore structures within the local landscape context, C) nearshore native fish CPU (NSNat) and the number of shore structures within the 100 km updrift landscape context, and D) nearshore introduced species CPU (NSInt) and the number of shoreline structures within the 50 km updrift landscape context.

(Table 9). In contrast, NSPis showed a nearly significant negative relationship with shore structures within the 50 km updrift buffer and a significant negative relationship with urban land use within the 100 km updrift buffer (Fig. 10a), while the smaller buffer contexts accounted for only moderate to very little variation in NSPis (Table 10). Mean NSPlk exhibited a nearly significant positive relationship with urban land use within the largest updrift landscape context (Fig. 10b). The smaller buffer contexts each accounted for <16% of the variation in NSPlk (Table 9). Shore structures of all landscape contexts explained <22% of the variation in NSPlk (Table 10). Mean NSBen was not significantly related to urban land uses of any landscape context, although the smallest landscape context explained the greatest degree of variability in NSBen (Table 9). Mean NSBen exhibited a significant negative relationship with shore structures of the local landscape context (Fig. 11b), and the degree of variability in NSBen explained by shore structures decreased with increasing landscape context (Table 10).

Mean NSNat and NSInt were not significantly related to urban land uses of buffers over all landscape contexts (Table 9). Among the landscape contexts, the 10 km and 25 km updrift described the greatest degree of variation in mean NSNat relative to urban land use (Table 9). Shore structures within buffers generally explained <22% of the variation in NSIntCPU (Table 9). Mean NSNat exhibited a significant negative relationship to the number of shoreline structures quantified over the largest landscape context (Fig. 11c), and very little variation in NSNat was explained in each of the smallest landscape context regression analyses (Table 10). NSInt exhibited a nearly significant negative relationship to shore structures of the 50 km updrift landscape context (Fig. 11d), and the smallest two landscape contexts explained <2% of the variation in mean NSInt (Table 10).

DISCUSSION

Fish, benthic macroinvertebrate, and zooplankton communities of eastern Lake Michigan bluff shorelines varied greatly within and among sites, and for benthos and zooplankton, between years. However, with the exception of Secchi depth, site physicochemical measures varied little among sites. Despite the variability in turbidity among sites, Secchi depths were statistically similar between shoreline classes and tended to increase with increasing latitude regardless of shoreline condition. This suggested that local shoreline condition was not a significant factor in determining the turbidity of adjacent nearshore waters. Turbidity reflects both organic and inorganic materials suspended in the water column, both of which influence biological communities in significant

ways. The absence of consistent patterning of nearshore turbidity with local shoreline condition suggests that local factors may not play a significant role in structuring nearshore communities via pathways mediated by suspended organic and inorganic materials (e.g., productivity), presumably due to the actions of alongshore currents. However, sediment and nutrient inputs from nearby updrift tributary confluences may have had significant influences on local nearshore communities of some sites. Although beyond the scope of this study, the potential for organic and inorganic materials associated with tributary confluences to influence local nearshore biological communities should be addressed in future research.

We expected benthic macroinvertebrate community measures to differ between shoreline classes, and the absence of significant differences in these measures was surprising. Although few historical studies exist that focus on relationships between nearshore benthos and shoreline environmental properties (e.g., Garza and Whitman 2004, Goforth and Carman *in press*), they do suggest that nearshore benthic communities respond to shoreline land use or manipulation at relatively local scales (i.e., <10 km). In contrast to the local shoreline analyses, the spatial analyses showed some agreement with these past studies by demonstrating that greater variability in BMTD was explained by urban land uses of the smaller landscape contexts (i.e., <25 km updrift) compared to larger landscape contexts (i.e., >50 km updrift). This is likely a result of local changes in sand distribution and stability mediated by shore structures similar to the findings of Garza and Whitman (2003). However, significant regressions of BMTD with the number of shore structures within the 50 km updrift landscape context also suggested that there may be cumulative influences of shore structures on local macrobenthos, presumably because of collective changes in substrate movement and distribution that influence local nearshore benthic habitats.

Sand substrates dominated almost every sampling station, suggesting similar habitat availability among sites. However, there were subtle differences in the particle sizes of these sands which were anecdotally noted, although not quantified as part of the study. These apparently subtle changes in substrate particle size likely constituted considerable differences in habitat availability from the perspective of benthic macroinvertebrates (Winnell and Jude 1984). Some nearshore sites were also characterized by pockets of accumulated organic debris that may have served as islands where benthos congregated due to the greater food resource availability within the larger context of the lake bed. The number, size, distribution, and availability of sand patches of differing particle sizes,

as well as organic debris islands, are likely to be of great importance in determining benthic productivity and distribution in nearshore zones. However, our sampling regime did not stratify according to substrate particle size or organic debris concentrations, and therefore high variability due to random sampling error may have masked responses of benthos to local changes in shoreline condition. Further research focusing on the relative importance of these microhabitat features is therefore important for better understanding how nearshore benthos are influenced by local habitats. In addition, studies focusing on the physical factors that determine the spatial distribution of such microhabitats within nearshore zones is needed to better understand how biologically relevant habitats are influenced by shoreline change.

Most benthic macroinvertebrates exhibited differences in densities between the study years, often by an order of magnitude in size. This was not surprising given that the 3.0 m depth contour of Great Lakes nearshore zones is subject to constant disturbance from wave and current activity (Garza and Whitman 2004), and it is likely that local aquatic communities fluctuate on daily, weekly, seasonal, and annual bases (Brazner and Beals 1997). The great variability in benthic macroinvertebrate densities between years suggests that long-term datasets reflecting annual, or even seasonal, variations in benthic communities are needed to better understand the how benthic communities respond to changes in nearshore environmental properties.

We were surprised to see very few instances of benthic ANS during our surveys. Only a few adult *Dreissena* sp. were observed among all samples, and no invasive amphipods were detected. This contrasts with Goforth and Carman's (*in press*) observations of high densities of dreissenids in nearshore zones along modified shorelines of Lake Erie and the western side of Lake Michigan. These nearshore areas were dominated by many large cobbles and boulders within a matrix comprised chiefly of clay, although the Lake Erie site is known to have been dominated by sand historically before shore structures designed to protect bluffs altered the substrate regime, diverting sand away from the nearshore zone (Meadows et al. *in press*). Large, hard substrates were almost entirely absent from our survey sites along the eastern Lake Michigan shoreline and likely contributed to the general absence of adult *Dreissena* sp., although veligers were observed rather prominently in zooplankton samples. Although dreissenids have been observed in some soft-bottomed habitats of the Great Lakes, the high energy of the nearshore zone of eastern Lake Michigan, combined with the lack of large, stable substrates, is likely to have interfered with successful settlement and subsequent

maturation of veligers. In comparison, dreissenids were present in large numbers in the quieter waters of drowned river mouths in close vicinity to the nearshore areas we surveyed (Plate 5). Thus, maintaining naturally active, dynamic sandy nearshore areas and shorelines likely helps to discourage the spread and establishment of dreissenids in these nearshore areas. However, continued and expanded modifications of the Lake Michigan shoreline may lead to a similar "sand starved" condition now apparent in other places of the basin (e.g., Garza and Whitman 2004, Meadows et al. *in press*), and thus potentially facilitate the establishment of current and future ANS.

It was not surprising that zooplankton community measures were similar between the shoreline classes and were not related to urban land uses or number of shore structures along shorelines at multiple spatial scales. Although zooplankton distributions are generally considered to be heavily dependent upon larger scale features of water bodies such as wind and current directions, there has also been some evidence to suggest that local zooplankton communities may be influenced by local nearshore environmental and ecological properties. High local densities of dreissenids can influence zooplankton densities via indirect competition for phytoplankton (Dettmers et al. 2003, Goforth and Carman *in press*). For example, nearshore zones that have become sand-starved as a result of shoreline land use and engineering can provide greater availability of substrates suitable for settling dreissenid veligers and can facilitate such localized changes in zooplankton communities (Goforth and Carman *in press*). However, localized shifts in plankton availability in response to feeding dreissenids was not a factor in this study for reasons explained earlier. Thus, a further benefit of maintaining nearshore areas that are naturally dominated by sand substrates is lowered susceptibility to dreissenid-mediated changes in food web structure.

Similar densities of the calanoid *L. macrurus* between shoreline classes was probably the most notable result based on zooplankton data analyses. *L. macrurus* is considered to be an indicator of oligotrophic conditions because it is a cold water stenotherm requiring high dissolved oxygen concentrations (Gannon and Stemberger 1978). This species has been used as an indicator of ecosystem recovery in the Lake Erie Basin due to its intolerance of cultural eutrophication (Kane et al. 2004), and its consistent presence and abundance in Lake Michigan samples included in the present study suggests that local shoreline condition does not significantly influence trophic condition of adjacent nearshore waters. However, it should be noted that current densities of *L. macrurus* are considerably lower than those reported historically for Lake Michigan

(Evans 1986), suggesting that there has been some loss of biological integrity in Lake Michigan based on the history of decline in this species. However, it appears that *L. macrurus* is currently distributed rather uniformly along the eastern Lake Michigan shoreline, suggesting that cumulative impacts, rather than specific shoreline reaches, are likely to be responsible for observed decreases in abundance.

Surprisingly few non-native zooplankton species were observed in this study. While densities of *C. pengoi* were very low during 2003 and 2004, this was the dominant zooplankton observed in samples collected at SJ during summer 2000 (Goforth et al. 2002). Reasons for this difference in abundance of *C. pengoi* between the two studies are unclear, although they may reflect greater current rates of predation on this species by planktivorous fish (Bushnoe et al. 2003). *Dreissena* sp. veligers were present at all sites, and the general absence of adult dreissenids suggests that veligers originated at updrift, offshore, or drowned river mouth locations. Very little habitat suitable for adult dreissenids was detected during reconnaissance visits updrift of the survey sites, suggesting that the primary sources for veligers were more likely from offshore locations and tributaries. While we cannot comment on occurrences of adult dreissenids in offshore locations, it was clear that extensive colonies of adults were present in the protected drowned river mouths (e.g., Plate 5). These populations likely served as sources for many of the veligers seen in nearshore zooplankton samples. However, as discussed earlier, very few adult dreissenids were observed in benthic samples and reconnaissance visits outside study areas, so the absence of suitable habitat in these sandy nearshore zones appears to be adequate for discouraging colonization by dreissenids.

Responses of fish communities to local shoreline condition and multi-scale anthropogenic properties of shoreline buffers were much more consistent with our expectations than either benthic macroinvertebrates or zooplankton. Our results generally concur with those of Kelso and Minns (1996) and Brazner and Beals (1997) in that larger fish tended to be more responsive to larger-scale shoreline features while smaller fish tended to be more responsive to smaller-scale shoreline properties. Larger fish species appear to be better at changing their movements and behaviors to take advantage of alternative habitats when others become sub-optimal, making them much less dependent upon specific local sites for long-term viability of populations (Kelso and Minns 1996). In contrast, smaller species are not capable of comparable changes in behavior, and are thus considered to be more influenced by local habitat changes (Schindler 1987). While this may superficially suggest that local site management is unimportant for

sustaining recreational and commercial fisheries that depend on nearshore habitats, small fish that are influenced by smaller scale phenomena nonetheless serve as important forage for the game species, and viability of these forage fish is therefore highly desirable. Thus, management strategies to enhance nearshore resource sustainability over multiple spatial scales will be needed to preserve not only valuable fisheries, but also native biodiversity and prey for game fish.

While the Secchi depth, benthic macroinvertebrate, and zooplankton analyses described previously did not appear to indicate significant differences in relative productivity between shoreline classes, SWPis and SWPlk were higher for nearshore areas adjacent to modified shorelines. NSPis CPU was also more closely related to smaller scale landscape contexts and may have reflected NSPis tracking of SWPlk as a prey resource. While SWPlk densities (as well as SWPis and NSPis) would be expected to be greater in response to increased local availability of phytoplankton and zooplankton that could result from increased nutrient loading from adjacent shoreline land uses, Secchi depth and zooplankton analyses did not suggest this to be the case in our study. It is possible that local zooplankton populations may fluctuate widely over the short term, while shallow water fish populations remain more constant over time, enduring zooplankton “feast or famine” cycles that were not detected in the current study or switching facultatively to other food sources (e.g., benthic invertebrates) when zooplankton become scarce. This residential existence hypothesis for small non-game fish could not be tested within the context of our study, although it does appear that these communities are more responsive to local vs. larger scale properties of shorelines, with the exception of cumulative shoreline influences that appear to operate at larger scales to negatively influence local shallow water fish communities. Few fish species were common to more than a few sites despite the relatively small geographic range of the study area and the considerable superficial similarity in habitat conditions among sites. However, it is worth noting that beach seine samples varied greatly, often even among replicate samples taken in relatively close proximity of one another. There may be more subtle changes in Great Lakes shallow water habitats that influenced local distributions of small non-game fish and juvenile game fish. As with benthos, more focused study of relationships between shallow water fish and potential microhabitats of Great Lakes nearshore zones is warranted.

While we expected *N. melanostomus* and other introduced fish species to be more abundant in nearshore waters adjacent to modified shorelines, this was not the case. *N. melanostomus* CPU was not different between

the shoreline classes, presumably because of the general similarity in shallow water habitat among all sites. In other locations where nearshore areas have become sand starved (e.g., central Lake Erie), habitat conditions have changed to become favorable for *N. melanostomus*, and it has become established as the dominant shallow water benthic species as a result (Meadows et al. *in press*). None of the sites included as part of this study exhibited evidence of sand starvation, and similar to adult dreissenids, suitable habitat for *N. melanostomus* was lacking at survey sites. Most individuals observed were small and may have been actively dispersing and/or displaced juveniles seeking appropriate habitat or occupying suboptimal habitat. As with dreissenids, populations of *N. melanostomus* in the drowned river mouths may have served as sources of juveniles that were then transported or moved to nearshore areas where they formed sink populations that were unstable and had low long-term viability. This provides another example of a case where maintenance of natural sand dynamics in these systems decreases the potential for establishment and spreading of ANS that depend on large, more stable substrates for habitat.

SUMMARY

Benthic macroinvertebrates and zooplankton communities did not exhibit significant responses to local shorelines, and most of the variation explained in these measures was attributed to urban land use and/or the number of shoreline structures within shoreline buffers of larger landscape contexts updrift from the study sites. In contrast, shallow water fish exhibited greater responses to smaller scale shoreline condition and urban land use, and nearshore piscivorous fish appeared to track with the prey fish patterns. However, fish communities also exhibited negative relationships with increasing numbers of shore structures within larger landscape contexts. These patterns of response suggest that nearshore food webs in sand-based systems integrate responses of multiple trophic levels to environmental properties operating at multiple spatial scales. Although the mechanisms influencing different components of the food web were not evident, there is little doubt that sustaining nearshore biodiversity of the Great Lakes will require management of resources at multiple spatial scales. The general absence of adult benthic ANS despite the availability of substantial pools of juvenile ANS in eastern Lake Michigan, including *N. melanostomus* and *Dreissena* sp., suggests that sand-based nearshore areas discourage successful colonization of these species due to the lack of large, stable substrates and high energy of the wave zone. This suggests that maintaining natural sand dynamics in the nearshore zones of eastern Lake Michigan should be a management priority.

ACKNOWLEDGEMENTS

We thank Amy Derosier, Rachel Harris, Colleen McLean, Jensen Rodney, and Frank Magyar for many long hours in the field conducting surveys and in the laboratory processing field samples. We also thank Stephanie Swart and Helen Enander for their support in developing the GIS data layers. We thank the Department of Fisheries and Wildlife at Michigan State University for allowing us to use the 18' Whaler that made our sampling of the nearshore zone of Lake Michigan possible. Finally, we thank the Michigan Great Lakes Protection Fund, the Michigan Department of Environmental Quality's Office of the Great Lakes and Coastal Zone Management Unit, and the National Oceanic and Atmospheric Administration for providing the generous financial support that made this work possible.

LITERATURE CITED

- Allan, J. D. and L. B. Johnson. 1997. Catchment-scale analysis of aquatic ecosystems. *Freshwater Biology* 37: 107-111.
- Beletsky, D., J.H. Saylor, D.J. Schwab. 1999. Mean summer circulation in the Great Lakes. *Journal of Great Lakes Research* 25: 78-93.
- Botts, P.S., B.A. Patterson, and D.W. Schloesser. 1996. Zebra mussel effects on benthic invertebrates: physical or biotic? *Journal of the North American Benthological Society* 15: 179-184.
- Brazner, J.C. 1997. Regional, habitat, and human development influences on coastal wetland and beach fish assemblages in Green Bay, Lake Michigan. *Journal of Great Lakes Research* 23: 36-51.
- Brazner, J.C. and E.W. Beals. 1997. Patterns in fish assemblages from coastal wetland and beach habitats In Green Bay, Lake Michigan: a multivariate analysis of abiotic and biotic forcing factors. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1743-1761.
- Busch, W.-D.N. and S.J. Lary. 1996. Assessment of habitat impairments impacting the aquatic resources of Lake Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Suppl. 1): 113-120.
- Bushnoe, T.M., D.M. Warner, L.G. Rudstam, and E.L. Mills. 2003. *Cercopagis pengoi* as a new prey item for alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*) in Lake Ontario. *Journal of Great Lakes Research* 29: 205-212.
- Daily, G.C., S. Alexander, P.R. Ehrlich, L. Goulder, J. Lubchenco, P.A. Matson, H.A. Mooney, S. Postel, S.H. Schneider, D. Tilman, and G.M. Woodwell. 1997. Ecosystem Services: Benefits Supplied to

- Human Societies by Natural Ecosystems. Issues in Ecology 2, Spring 1997, published by the Ecological Society of America. 16 pp.
- Dermott, R. and D. Kerec. 1997. Changes to the deepwater benthos of eastern Lakes Erie since the invasion of *Dreissena*: 1979-1993. Canada Journal of Fisheries and Aquatic Sciences 54: 922-930.
- Dettmers, J.M., M.J. Raffenberg, J. Matthew, and A.K. Weis. 2003. Exploring zooplankton changes in southern Lake Michigan: implications for yellow perch recruitment. Journal of Great Lakes Research 29(2): 355-364.
- Duarte, C.M. and J. Kalff. 1990. Patterns in the submerged macrophyte biomass of lakes and the importance of the scale of analysis in interpretation. Canadian Journal of Fisheries and Aquatic Sciences 47: 357-363.
- Dunson, W.A. and J. Travis. 1991. The role of abiotic factors in community organization. American Naturalist 138: 1067-1091.
- Eadie, J. M. and A. Keast. 1984. Resource heterogeneity and fish species diversity in lakes. Canadian Journal of Zoology 62: 1689-1695.
- Environmental Systems Research Institute. 2004. ArcView Version 3.2. Redlands, CA.
- Evans, M.S. 1986. Recent major declines in zooplankton populations in the inshore region of Lake Michigan: probable causes and implications. Canadian Journal of Fisheries and Aquatic Sciences 43: 154-159.
- Frissel C.A., W.J. Liss, C.E. Warren and M.D. Hurley. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10: 199-214.
- Gannon, J.E. and R.S. Stemberger. 1978. Zooplankton (especially crustaceans and rotifers) as indicators of water quality. Transactions of the American Microscopical Society 97: 16-35.
- Garza, E.L. and R.L. Whitman. 2004. The nearshore benthic invertebrate community of southern Lake Michigan and its response to beach nourishment. Journal of Great Lakes Research 30: 114-122.
- Gergel, S.E., M.G. Turner, J.R. Miller, J.M. Melack, and E.H. Stanley. 2002. Landscape indicators of human impacts to riverine systems. Aquatic Sciences 64: 118-128.
- Goforth, R.R., D. Stagliano, J. Cohen, M. Penskar and Y.M. Lee. 2002. Biodiversity Analysis of Selected Riparian Ecosystems within a Fragmented Landscape, Phase II. Michigan Natural Features Inventory Report Number 2002-26. Prepared for the Michigan Great Lakes Protection Fund, Michigan Department of Environmental Quality, Office of the Great Lakes, Lansing, MI. 126 pp.
- Goforth, R.R. and S.M. Carman. *In Press*. Nearshore community characteristics related to shoreline properties in the Great Lakes. Journal of Great Lakes Research.
- Goforth, R.R., S.M. Carman, S.D. Mackey, J. Fuller, D. Guy, and D. Liebenthal. 2002. Ecological Characteristics of Nearshore Areas Along Six Great Lakes Shorelines. Michigan Natural Features Inventory Report Number 2002-19. Prepared for the Great Lakes Protection Fund, Chicago, IL. 44pp.
- Goforth, R.R. and S.M. Carman. 2003. Research, Assessment, and Data Needs to Promote Protection of Great Lakes Nearshore Fisheries Habitat. Proceedings of a workshop conducted on April 1-2, 2003, Muskegon, MI.
- Goodyear, C.D., T.A. Edsall, D.M. Ormsby-Dempsey, G.D. Moss, and P.E. Polanski. 1982. Atlas of spawning and nursery areas of Great Lakes fishes. FWS/OBS-82/52. Volumes 1-14. Washington, DC, USFWS.
- Haynes, J.M., T.W. Stewart, and G.E. Cook. 1999. Benthic macroinvertebrates communities in southwestern Lake Ontario following invasion of *Dreissena*: continuing change. Journal of Great Lakes Research 25(4): 828-838.
- Hynes, H.B.N. 1975. The stream and its valley. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 19: 1-15.
- Izvekova, E.I. and A.A. Lvova-Katchanova. 1992. Sedimentation of suspended matter by *Dreissena polymorpha* Pallas and its subsequent utilization by Chironomidae larvae. Polish Archive of Hydrobiology 19:203-210.
- Jude, D.J. and F.J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 42: 1154-1157.
- Kane, D.D., J.E. Gannon, and D.A. Culver. 2004. The status of *Limnocalanus macrurus* (Copepoda: Calanoida: Centropagidae) in Lake Erie. Journal of Great Lakes Research 30: 22-30.
- Kelso, J.R.M. and C.K. Minns. 1996. Is fish species richness at sites in the Canadian Great Lakes the result of local or regional factors? Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 175-193.
- Kelso, J. R. M. and K. I. Cullis. 1996. The linkage among ecosystem perturbations, remediation and the success of the Nipigon Bay fishery. Canadian Journal of Fisheries and Aquatic Sciences 53 (Suppl. 1).

- Kelso, J.R.M., R.J. Steedman, and S. Stoddart. 1996. Historical causes of change in Great Lakes fish stocks and the implications for ecosystem rehabilitation. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Suppl. 1): 10-19.
- Krieger, K.A. 1984. Benthic macroinvertebrates as indicators of environmental degradation in the southern nearshore zone of the central basin of Lake Erie. *Journal of Great Lakes Research* 10: 197-209.
- Lane, J.A., C.B. Portt, and C.K. Minns. 1996. Nursery habitat characteristics of Great Lakes fishes. *Canadian Manuscript Report of Fisheries and Aquatic Sciences* 2338.
- Lane, J.A., C.B. Portt, and C.K. Minns. 1996. Habitat characteristics of adult fishes of the Great Lakes. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*.
- Leslie, J.K. and C.A. Timmins. 1993. Distribution, density, and growth of young-of-the-year fishes in Mitchell Bay, Lake St. Clair. *Canadian Journal of Zoology* 71: 1153-1160.
- Madenjian, C.P., G.L. Fahnenstiel, T.H. Johengen, T.F. Nalepa, H.A. Vanderploeg, G.W. Fleischer, P.J. Schneeberger, D.M. Benjamin, E.B. Smith, J.R. Bence, E.S. Rutherford, D.S. Lavis, D.M. Robertson, D.J. Jude, and M.P. Ebener. 2002. Dynamics of the Lake Michigan food web, 1970-2000. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 736-753.
- MacIsaac, H.J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. *American Zoologist* 36: 287-299.
- McDowall, R.M. 1996. Diadromy and the assembly and restoration of riverine fish communities: a downstream view. *Canadian Journal of Fisheries and Aquatic Sciences* 53(Suppl. 1):
- McMahon, G. and D.A. Harned. 1998. Effect of environmental setting on sediment, nitrogen, and phosphorus concentrations in Albemarle-Pamlico drainage basin, North Carolina and Virginia. *Environmental Management* 22: 887-903.
- Meadows, G.A., D.M. Mickelson, T.B. Edil, R.R. Goforth, S.D. Mackey, J. Fuller, D. Guy, L.A. Meadows, E. Brown, and S.M. Carman. *In Press*. Cumulative impacts of nearshore engineering. *Journal of Great Lakes Research*.
- Mills, E.L., J.H. Leach, J.T. Carlton, and C.L. Secor. 1993. Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* 19: 1-54.
- Minns, C.K. 1989. Factors affecting fish species richness in Ontario lakes. *Transactions of the American Fisheries Society* 118: 533-545.
- Osborne, L.L. and M.J. Wiley. 1992. Influence of tributary spatial position on the structure of warmwater fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 671-681.
- Randall, R. G. and C.K. Minns. 2002. Comparison of a habitat productivity index (HPI) and an index of biotic integrity (IBI) for measuring the productive capacity of fish habitat in nearshore areas of the Great Lakes. *Journal of Great Lakes Research* 28: 240-255.
- Ratti, C. and D.R. Barton. 2003. Decline in the diversity of benthic invertebrates in the wave-zone of eastern Lake Erie, 1974-2001. *Journal of Great Lakes Research* 29: 608-615.
- Reeves, G.H., F.H. Everest, and J.R. Sedell. 1993. Diversity of juvenile anadromous salmonid assemblages in coastal Oregon basins with different levels of timber harvest. *Transactions of the American Fisheries Society* 122: 309-317.
- Ricciardi, A., F.G. Whoriskey, and J.B. Rasmussen. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2596-2608.
- Ricciardi, A. and H.J. MacIsaac. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *TREE* 15: 62-65.
- Richards, C., L.B. Johnson, and G.E. Host. 1997. Catchment and reach-scale parameters as indicators of macroinvertebrate species traits. *Freshwater Biology* 37: 219-230.
- Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science* (Washington, D.C.) 235: 167-171.
- Roth, N.E., J.D. Allan, and D.E. Erickson. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. *Landscape Ecology* 11: 141-156.
- Schindler, D.W. 1987. Detecting ecosystem response to anthropogenic stress. *Canadian Journal of Fisheries and Aquatic Sciences* 44: 6-25.
- Soranno, P.A., S.L. Hubler, S.R. Carpenter, and R.C. Lathrop. 1996. Phosphorus loads to surface waters: a simple model to account for spatial pattern of land use. *Ecological Applications* 6: 865-878.
- Steedman, R.J. and H.A. Regier. 1987. Ecosystem science for the Great Lakes: perspectives on degradative and rehabilitative transformations. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Suppl. 2): 95-103.
- Stewart, T.W., J.G. Miner, and R.L. Lowe. 1998. Macroinvertebrate communities on hard substrates in western Lake Erie: structuring effects of *Dreissena*. *Journal of Great Lakes Research* 24(4): 868-879.

- Thayer, S.A., R.C. Haas, R.D., and R.H. Kushler. 1997. Zebra mussel (*Dreissena polymorpha*) effects on sediment, other zoobenthos, and the diet and growth of adult yellow perch (*Perca flavescens*) in pond enclosures. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1903-1915.
- Vanderploeg, H.A., T.F. Nelepa, D.J. Jude, E.L. Mills, K.T. Holeck, J.R. Leibig, I.A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1209-1228.
- Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130-137.
- Weaver, L.A. and G.C. Garman. 1994. Urbanization of a stream and historical changes in a stream fish assemblage. *Transactions of the American Fisheries Society* 123: 162-172.
- Weller, D.E., T.E. Jordan, and D.L. Correll. 1998. Heuristic models for material discharge from landscapes with riparian buffers. *Ecological Applications* 8: 1156-1169.
- Wei, A., P. Chow-Fraser, and D. Albert. 2004. Influence of shoreline features on fish distribution in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1113-1123.
- Whillans, T.H. 1979. Historic transformations of fish communities in three Great Lakes bays. *Journal of Great Lakes Research* 5: 195-215.
- Whittier, T.R., R.M. Hughes, and D.P. Larsen. 1988. Correspondence between ecoregions and spatial patterns in stream ecosystems in Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 45: 1264-1278.
- Wichert, G.A. 1995. Effects of improved sewage effluent treatment and urbanization on fish associations of Toronto streams. *North American Journal of Fisheries Management* 15: 440-456.
- Winnell, M.H. and D.J. Jude. 1984. Associations among Chironomidae and sandy substrates in nearshore Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 174-179.

COLOR PLATES



Plate 1. An example of a modified shoreline near Saint Joseph, Michigan, with commercial land use and extensive shore structure development. Loss of vegetation on areas of the bluff have caused high levels of erosion and soil loss.



Plate 2. An example of a largely intact shoreline near Ludington, Michigan.



Plate 3. Removal of benthic samples from the Petite Ponar dredge prior to preservation in ethanol.



Plate 4. Deployment of the zooplankton net to collect vertical plankton tows at the 3.0 m depth contour of study sites.



Plate 5. Zebra mussel clusters and individuals attached to a gastropod shell and leaves of *Vallisneria americana* found in the drowned river mouth of the Pere Marquette River where it joins with Lake Michigan.

